UNIVERSITÀ DEGLI STUDI DI FIRENZE

DIPARTIMENTO DI BIOLOGIA EVOLUZIONISTICA "L. Pardi"

DOTTORATO DI RICERCA IN ETOLOGIA, ECOLOGIA ANIMALE E ANTROPOLOGIA
(XXV CICLO, BIO 05, BIO 07)

Ecology and behaviour of *Velia currens* and *V. gridellii* (Hemiptera: Heteroptera: Veliidae)

Tesi di

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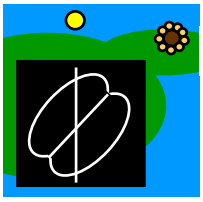
(2012)



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1. ABSTRACT

Velia currens (Fabricius, 1794) and *V. gridellii* Tamanini, 1947 are two Alpine-Apenninic endemic insects, and little is known about their ecology and behaviour.

A key with field identification characters was created for the subsequent ecological studies, and the analysis of several morphological features defined the species groups within the subgenus *Plesiovelia* Tamanini, 1955 for the first time. The two species appeared to belong to different groups.

The ecological studies investigated life histories, quantified occurrence of wing polymorphism and gathered information regarding the degree of co-occurrence of the two species. No evidence for multivoltinism was detected in either species. However, oviposition and and/or hatching continued up to midsummer. The two species are dimorphic, but winged specimens were rarely recorded. An important discovery was the presence, during summer, of adults of both sexes hidden beneath the stones of dried-up streams. This aestivation in an apparent state of lethargy may reduce the advantages associated with producing winged forms and could account for the low rate of occurrence of macropterism in these species. Finally, although the distributional ranges of the two taxa completely overlap on a large spatial scale, they co-occurred only rarely at the same sites and the degree of co-occurrence was lower than expected by chance.

The descriptions and SEM images of the hairy structures of the two taxa were planned as essential to the study of the "grooming behaviour". The comparison between these two species and *V. caprai* Tamanini, 1947, the only other known species of the genus, comfirmed a substantial homogeneity within the subgenus *Plesiovelia*. The discovery of a double layer of microtrichia in both our species allowed us to detect them in *V. caprai* too, for which only a single layer had previously been described. Finally, we report for the first time in the genus, and in the Old World Veliinae, the presence in the females of *V. gridellii* of a structure corresponding to the grasping comb already described in males. A similar structure was not identified in *V. currens*. Considering the species groups, this difference may be relevant to a better understanding of the relationships among species belonging to this genus.

The "grooming behaviour", a series of cleaning actions performed to tidy the waterproofing hair layers throughout the body surfaces and maintain them free from debris, was described. Results showed that this behavior may be highly variable even within the same species, with some steps sometimes being skipped, suggesting that once the "pattern" has started, this action is not modulated by way of feedback from the area that has been cleaned. The behaviour is, however, extremely similar in the two species, and only a few differences were noticed such as a different number of passages over the antennae.

A peculiar behaviour, observed under natural and laboratory conditions in both the species, consists in interactions ("collisions") among the specimens and was named "contact behaviour". Preliminary observations on *Velia gridellii*

Tamanini, 1947, through the analysis of the networks representing the contacts between specimens of this aquatic insect, did not allowed to evidence any difference between males and females, neither in their degree of connection with other specimens, nor in the role they played.

2. INTRODUCTION

Velia currens (Fabricius, 1794) and *V. gridellii* Tamanini, 1947 are two Alpine-Apenninic endemic Hemiptera Heteroptera ("true bugs"). Both are common species in Italy, but they are absent on the islands (except for *V. gridellii* which is presente on the Isle of Elba). *V. currens* is distributed throughout the entire Alpine area, while *V. gridellii* is restricted to the Prealps; in the southern part of their distribution area both reach Calabria (Tamanini, 1979; cf. Bacchi and Rizzotti Vlach, 2005).

These insects belong to the Gerromorpha, known as "semi-aquatic bugs" (Andersen, 1982) because their life-cycle is strongly associated with water at all life stages. *Velia currens* and *V. gridellii* are gregarious insects, usually occurring in "schools" of individuals in the shaded and calm waters of streams, where they catch prey (general predators) floating on the water by means of their strong forelegs (Poisson, 1957; Andersen, 1982; Cianferoni and Santini, 2012)

Like other Gerromorpha, *Velia* spp. show tarsal modifications to facilitate locomotion on the surface tension layer of the water (the claws can be retracted in a lateral niche so as not to break the surface tension), and they have dense coatings of setae and microtrichia on various parts of the body that repel water (Tamanini, 1979; Heckman, 1983). When on a water surface these insects move by rowing (synchronous moving of the middle legs; Fig. 1); when on land, they move like other terrestrial insects (Andersen, 1995).

They are heterometabolous paurometabolous insects, with five larval instars similar to apterous adults (Tamanini, 1979; Fig. 2). The two case studies are dimorphic, with both apterous and macropterous (very rare) forms. The dark membranous fore wings show white spots and markings. Eggs are set on plants or floating leaves just out of the water (Tamanini, 1947; Fig. 3). Adults overwinter on the banks, under stones or debris (Tamanini, 1979). They have an holopneustic respiratory system similar to terrestrial bugs, with spiracles through which the air enters and leaves, and internal chambers for gas exchange (Tamanini, 1979).

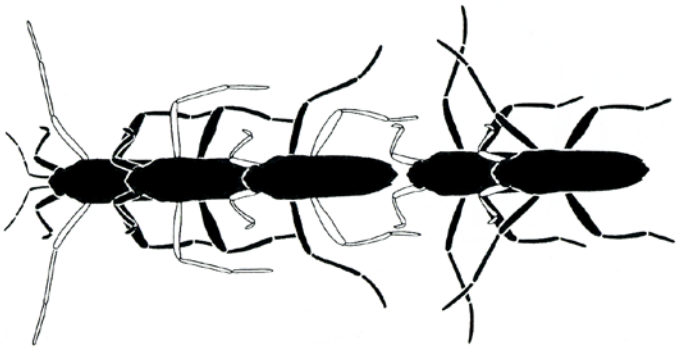

Fig. 1. Locomotion on the water surface. Supporting legs shown black. Modified from Andersen (1976).

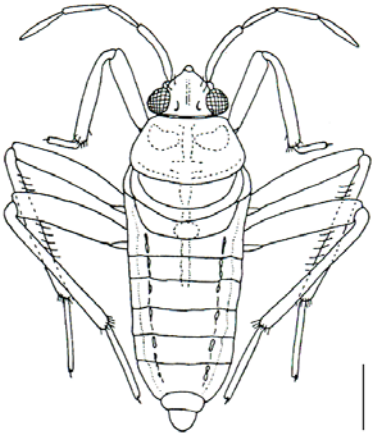

Fig. 2. Fifth instar nymph of *Velia gridellii* Tamanini, 1947 (scale bar, 1 mm). Modified from Tamanini (1979).

Fig. 3. Egg of *Velia gridellii* Tamanini, 1947. (scale bar, 0.5 mm). Modified from Tamanini (1979).

2.1 Systematics

Velia currens (Fabricius, 1794) and *V. gridellii* Tamanini, 1947 belong to the order Hemiptera Linnaeus, 1758; suborder Heteroptera Latreille, 1810, infraorder Gerromorpha Popov, 1971; family Veliidae Brullé, 1836; subfamily Veliinae Brullé, 1836.

The order, besides Heteroptera, also includes four other monophyletic suborders: Coleorrhyncha, Cicadomorpha, Fulgoromorpha and Sternorrhyncha (Bourgoin and Campbell, 2002). Heteroptera, or “true bugs”, are part of the most successful radiation of nonholometabolous insects, and contain seven other monophyletic taxa, to date identified as infraorders (Weirauch and Schuh, 2011; Li et al. 2012).

The infraorder Gerromorpha has been recognized as a well-defined group since Dufour (1833) divided it from the Geocorisae of Latreille with the name Amphibicorisae (modern-day Gerromorpha). Its monophyly was confirmed by recent genetic studies (Li et al., 2012; Fig. 4) that, however, could not yet define their correct place inside the Heteroptera.

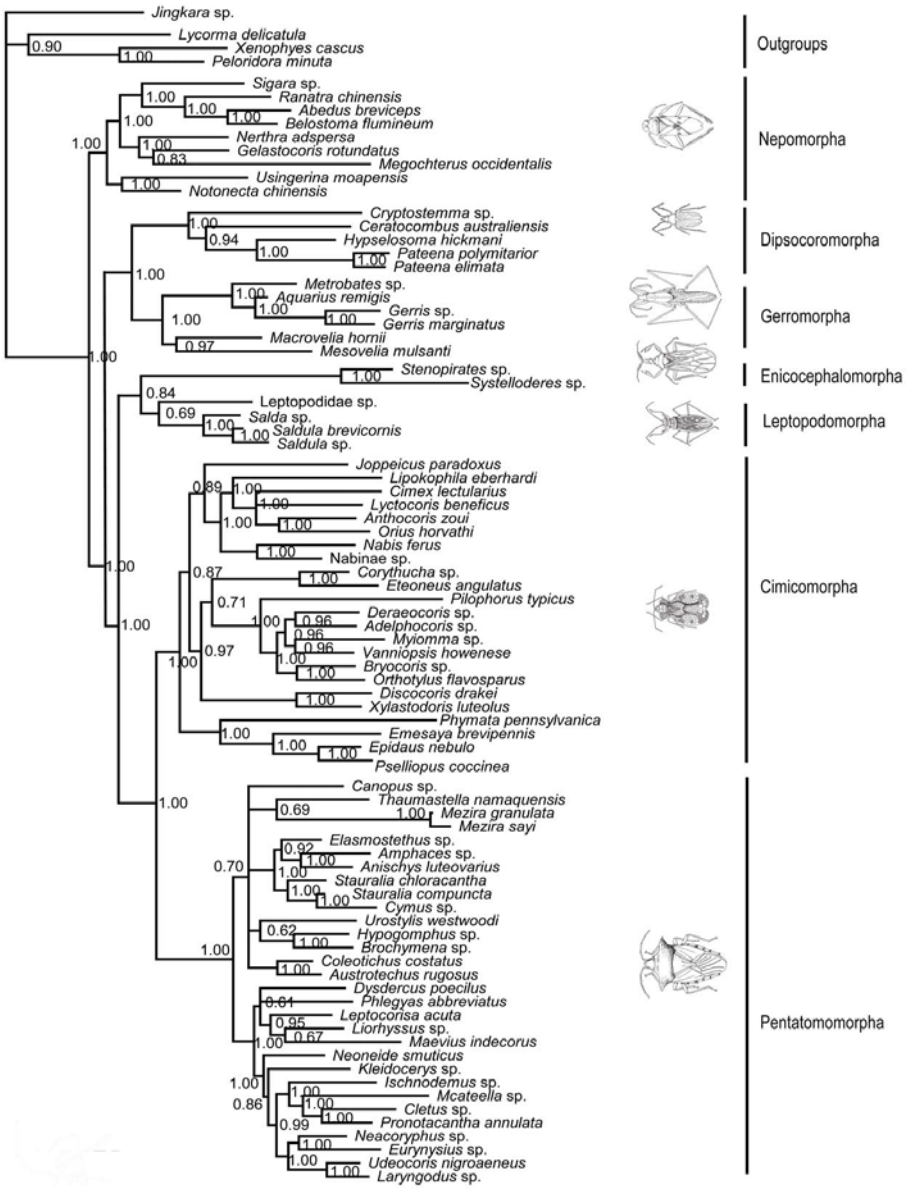

Fig. 4. Bayesian phylogram inferred from combined data set. Bayesian posterior probabilities (>50%) are indicated at each node. From Li et al. (2012).

Among Gerromorpha (Fig. 5) the Veliidae is a large and fairly diverse family, in which the subfamily Veliinae seems to be a monophyletic group (Andersen, 1982; Fig. 6).

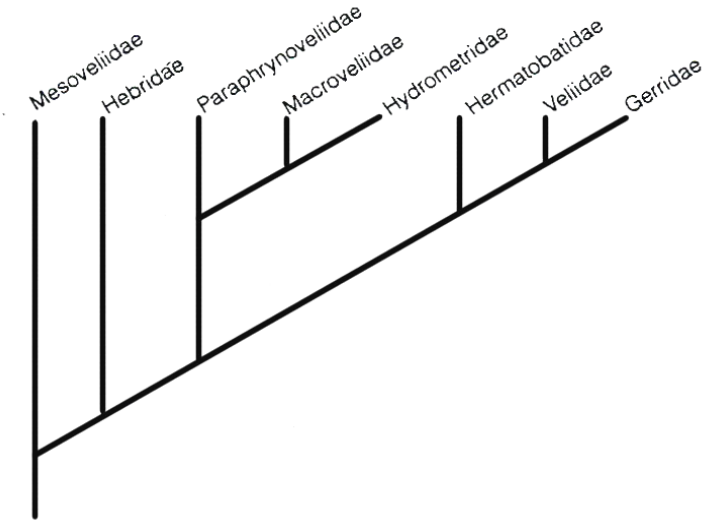

Fig. 5. Phylogenetic relationship of families of Gerromorpha. Modified from Schuh and Slater (1995).

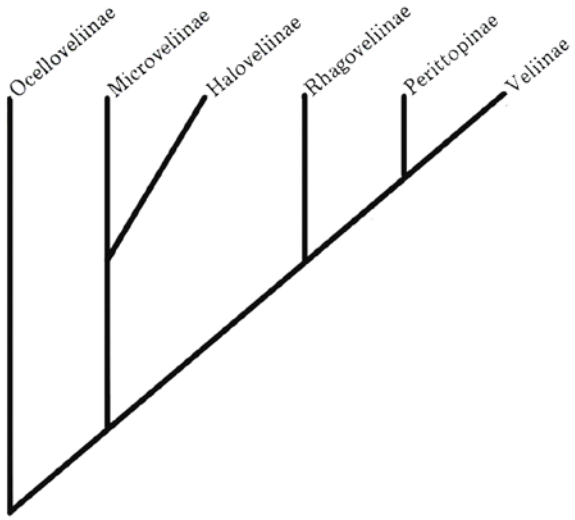

Fig. 6. Cladogram of realtionships between the subfamilies of Veliidae. Modified from Andersen (1982).

The mainly Palaearctic genus *Velia* Latreille, 1804 (26 species) is considered monophyletic due to the structure of the female proctiger (Andersen, 1982).

The two species analyzed here are included in the subgenus *Plesiovelia* Tamanini, 1955 mainly due to the structure of male genitalia and the morphology of antennae, metafermurs and metatrochanters (cf. Andersen, 1981).

2.2 Current status of knowledge

Among Gerromorpha, including over 2,100 described species (Polhemus and Polhemus, 2008), Gerridae is the most studied family (cf. Andersen, 1982).

The family Veliidae, with almost 1,000 described species, is the largest among Gerromorpha, while Gerridae counts less than 800 species; other families include a distinctly lower number of taxa. In the Palaearctic Region the two families show a similar number of species, 51 noted for Gerridae and 44 for Veliidae (Polhemus and Polhemus, 2008); the same occurs in Italy, with 13 and 11 spp. respectively (Bacchi and Rizzotti Vlach, 2007).

The taxonomic knowledge of aquatic and semiaquatic Heteroptera can be considered good for the Palaearctic Region (cf. Polhemus and Polhemus, 2007), especially in the W-Palaearctic where the knowledge of extant Gerromorpha, Nepomorpha and Leptopodomorpha is nearly complete.

An essential morphology-based taxonomical revision of the genus *Velia* Latreille was conducted by Tamanini (1947), and subsequently completed by further contributions (e.g. Tamanini, 1949; 1955). These works greatly improved the European and Italian knowledge of this genus.

Andersen's (1982) monograph was a real milestone in terms of phylogeny, adaptations, biogeography, and classification of Gerromorpha. This comprehensive work does not however consider all of the species for each family, and does not include the two species examined here; the subgenus *Plesiovelia* Tamanini, 1955 was represented only by *V. affinis* Kolenati, 1856 and *V. caprai* Tamanini, 1947. The same work summarized studies of locomotion (Andersen, 1976) and research on the fine structure of the body hair layers and morphology of the spiracles of semiaquatic bugs (Andersen, 1977), in which this author use *V. caprai* as the model-species for the family Veliidae.

Among the West Palaearctic Gerromorpha, the most widely studied family, in term of ecological studies, is Gerridae (see Spence and Andersen, 1994 and Ditrich and Papáček, 2009a for reviews), whereas other families, such as Veliidae, received less attention until recently (Ditrich et al., 2008, 2011; Ditrich and Papáček, 2009a, b, 2010a, b; Ditrich and Koštál, 2011; Cianferoni and Santini, 2012). Furthermore, most of the available information on Veliidae refers to species from Northern and Central Europe (e.g. Ekblom, 1926;

Mielewczyk, 1980; Murray and Giller, 1991), whilst little or nothing is known about the more southerly distributed taxa (Cianferoni and Santini, 2012).

The available literature on the genus *Velia* relates almost exclusively to the centralnorthern European species *Velia caprai* Tamanini, 1947 (e.g. Brinkhurst, 1959; Ditrich and Papáček, 2009b), whilst a few data also refer to *V. saulii* Tamanini, 1947 (Southwood and Leston, 1959; Mielewczyk, 1980).

Information about the biology and ecology of *Velia currens* (Fabricius, 1794) and *V. gridellii* Tamanini, 1947 is typically sparse and scattered in literature; general notes on Gerromorpha, Veliidae and sometimes on the genus *Velia* can be found in Poisson (1957) and Tamanini (1979).

Research on physiology was only conducted on *Velia caprai* Tamanini, 1947 (e.g. Meyer, 1971a, 1971b, 1974).

A few isolated studies have been carried out on parasites of species from the genus *Velia*, discovering trypanosomatids (*Crithidia gerridis* (Patton, 1908)); microsporidians (*Nosema veliae* Poisson, 1929); and nematodes (*Bradynema veliae* Poisson, 1933), isolated from *V. saulii* Tamanini, 1947 (Poisson, 1957).

It is noteworthly to mention Rensing's work (1962) on morphology, physiology and ethology, where he describes for the first and only time the "grooming" behaviour in Gerromorpha (as "Putzbewengungen" = cleaning movements), with *Velia caprai* being among the species examined.

The studies on orientation by Birukow (1957) and Birukow and Bush (1957) report observations on *Velia currens* in Germany. Because of the sampling location these studies must however refer to other species of the genus *Velia* (probably *V. caprai* or *V. saulii*) because *V. currens* has a different distribution.

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3. AIMS

Velia currens (Fabricius, 1794) and *V. gridellii* Tamanini, 1947 are two species of Veliidae from southern Europe, whose ecology and behaviour are poorly known (see Chapter 2.2).

The aim of this research was to begin to fill this gap through the study of different aspects of these two endemic species.

Firstly, a taxonomical study, based mainly on SEM imagery, was carried out in order to verify the validity of the species and support the choice of these case-studies. A set of field identification characters has been defined in detail for the ecological studies (Chapter 4.1).

The analysis of several morphological features was performed in order to define the species groups within the subgenus *Plesiovelia* (Chapter 4.2).

The aims of the ecological studies were to investigate life histories, to find evidence of multivoltinism, to quantify occurrence of wing polymorphism and to examine the degree of co-occurrence of the two species (Chapter 4.3).

The descriptions, through SEM analysis, of the hairy structures of the two taxa (Chapter 4.4) were a necessary pre-requisite to the study of “grooming behaviour” (Chapter 4.5).

Finally, preliminary observations on another peculiar behaviour (named “contact behaviour”) were tested, through the networks analysis, on *Velia gridellii* (Chapter 4.6).

4. RESULTS

4.1 Field identification characters and notes on the validity of the species

V. currens (Fabricius, 1794) and *V. gridellii* Tamanini, 1947 (Hemiptera: Heteroptera: Veliidae): field identification characters and notes on the validity of the species.

Introduction

The first described species of Veliidae was *Cimex rivulorum* Fabricius, 1775 [= *Velia* (*Velia*) *rivulorum* (Fabricius, 1775)], published in the "Systema Entomologiae". In 1794 it was moved from *Cimex* into *Gerris* and its previous diagnosis was repeated, unchanged, together with other two new species: *Gerris apterus* Fabricius, 1794 [syn. *Velia* (*Velia*) *rivulorum* (Fabricius, 1775)] and *Gerris currens* Fabricius, 1794 [= *Velia* (*Plesiovelia*) *currens* (Fabricius, 1794)] described on specimens from Italy. These three species were present in the "Systema Rhyngotorum" (Fabricius, 1803) within the genus *Hydrometra* Fabricius. The following year Latreille (1804) finally moved the three species into the genus *Velia*.

Until Tamanini's revision (1947), descriptions of the genus *Velia* have been made on the basis of ambiguous characters, such as color variations or other secondary and highly variable external features.

Moreover, several authors modified and extended the diagnosis of Fabricius's species without studying the types, thus introducing new errors. Only through the study of sexual characters (endososmal sclerites in particular) is it possible to clearly define the species. Tamanini (1947, 1949, 1955) defined the species of *Velia* Latreille hitherto described and also described several new species. The exact identity of *Velia currens* was established by Brown (1951), involving a comparison with Fabricius' material. The types of this species, in Allioni's collection have been destroyed, so Tamanini (1955) based the neotype of the species on a specimen from Fabricius' collection which was labeled as "*currens*".

Velia gridellii was described by Tamanini (1947) in the first revision of the genus. Later, specimens of *V. gridellii* were discovered in Fabricius' material, misidentificated as *V. currens* (Fabricius, 1794).

The two species were well defined by Tamanini (1947) mainly on the basis of male genitalia and the shape of the 9th tergite in both sexes.

Herein further studies on morphological characters also evidentiated by the scanning electron microscope (SEM) are presented, and I also give provide characters to separate the two species in the field, which are also useful for ecological studies (cf. Cianferoni and Santini, 2012).

Material and methods

Adult specimens of both sexes (apterous morph) were collected in several sites in the Florence and Arezzo provinces (Tuscany, Italy). The specimens, preserved in 70% alcohol, were cleaned with pure ethanol and dissected under a stereomicroscope. Selected pieces were mounted on aluminium supports (stubs) covered by conductive glue and sputter-coated with graphite and gold. The samples were observed using a Zeiss Evo MA15 scanning electron microscope at the Interdepartmental Center on Electron Microscopy and Microanalysis (M.E.M.A.) of the University of Florence. Further images were done with a stereomicroscope Konus Crystal-45.

Results

The two species can be separated by the structure of parameres (Figs 1–3) that clearly differ from other Italian species, whilst the shape of 9th tergite is useful only in the istance of *Velia currens* (Fabricius, 1794).

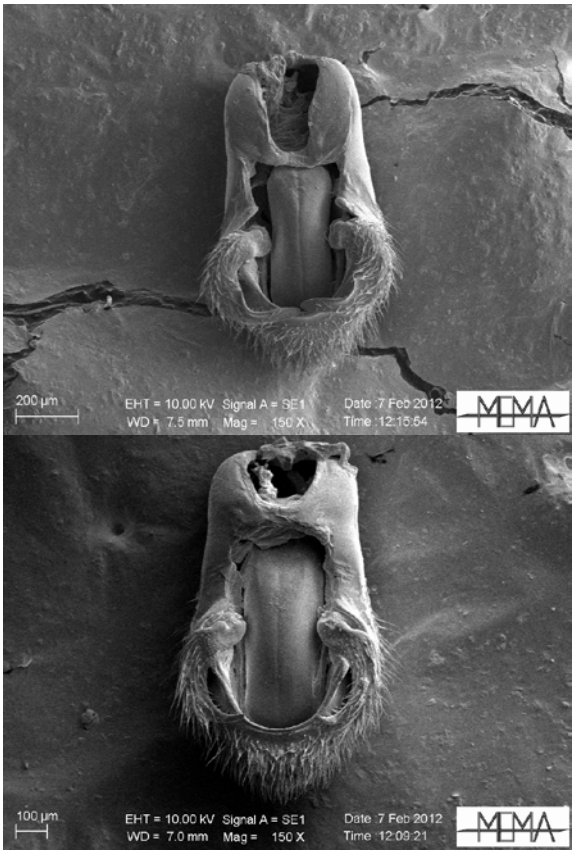

Fig. 1. Overview of the genital capsule of *Velia currens* (Fabricius, 1794) (top) and *V. gridellii* Tamanini, 1947 (bottom).

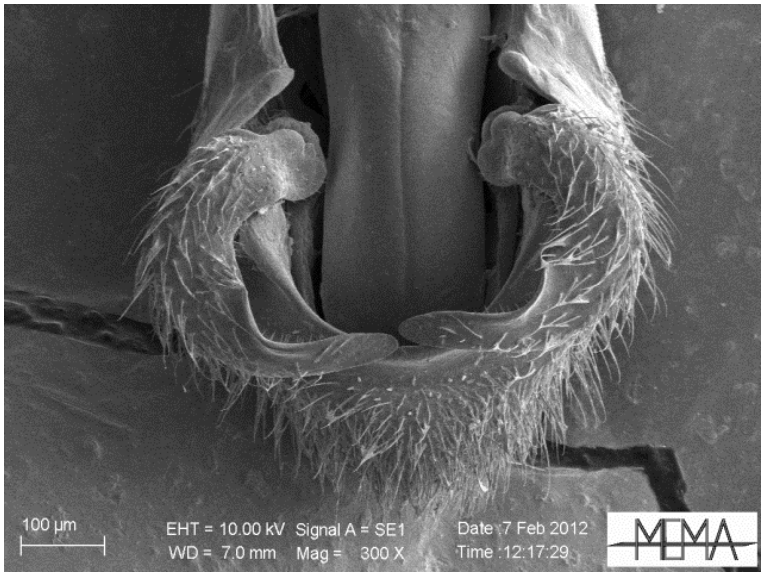

Fig. 2. Parameres of *Velia currens* (Fabricius, 1794).

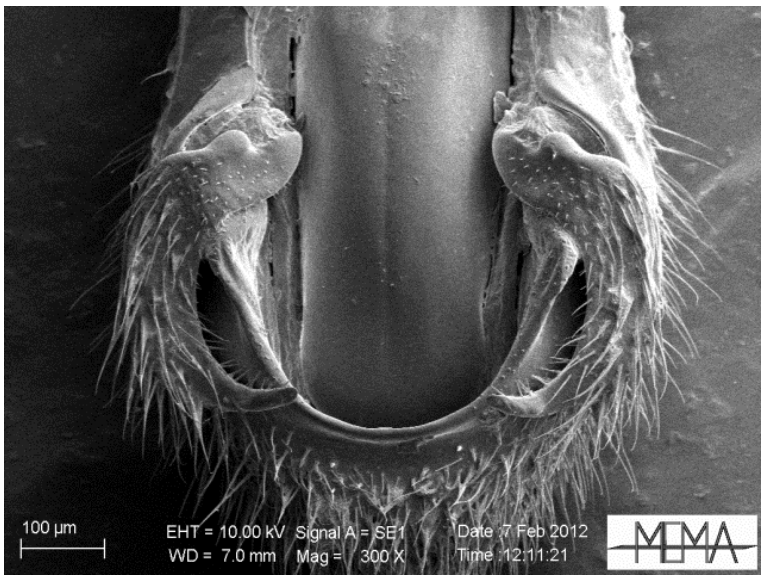

Fig. 3. Parameres of *Velia gridellii* Tamanini, 1947.

The trapezoidal shape of the 9th abdominal tergite, observed from behind in the female and dorsally in the male, allows us to immediately separate

V. currens from all other species of the genus. The only species with a enlarged 9th tergite in its female is *Velia muelleri* Tamanini, 1947, well recognizable by the upward-directed abdomen (distal parts of the abdomen face downward in *V. currens*).

Female specimens of *Velia gridellii* are immediately recognizable both by the strongly upward-directed abdomen, with its typical "saber" shape (Tamanini, 1979) and by the rounded 9th tergite. *Velia muelleri* Tamanini, 1947 also has an upward-directed abdomen, but can be easily separated (in the apterous specimens) by the enlarged 1st tergite protruding beyond the connexivum to form a small cone (Tamanini, 1947; Fig. 4) or in both morphs by the different shape of the 9th tergite (rounded in *V. gridellii* and enlarged in *V. muelleri*).

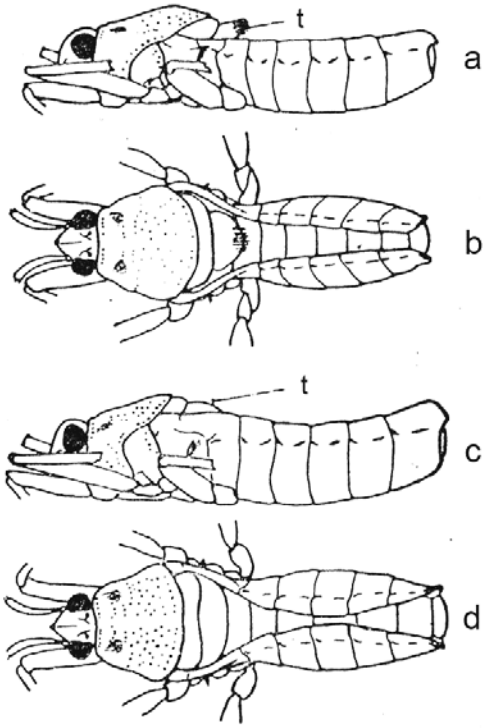

Fig. 4. Comparison between females of *Velia muelleri* Tamanini, 1947 (a, b) and *V. gridellii* Tamanini, 1947 (c, d). Later view (a, c) and dorsal view (b, d). t = 1st abdominal tergite. Modified from Tamanini (1947).

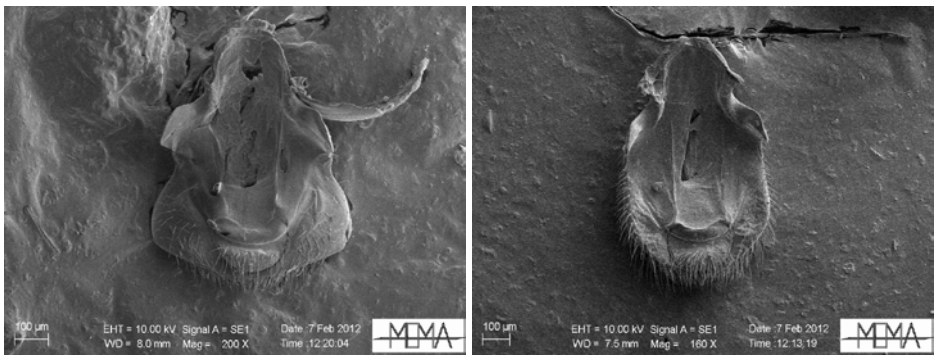

Fig. 5. Male 9th tergite of *Velia currens* (Fabricius, 1794) (left) and *V. gridellii* Tamanini, 1947 (right).

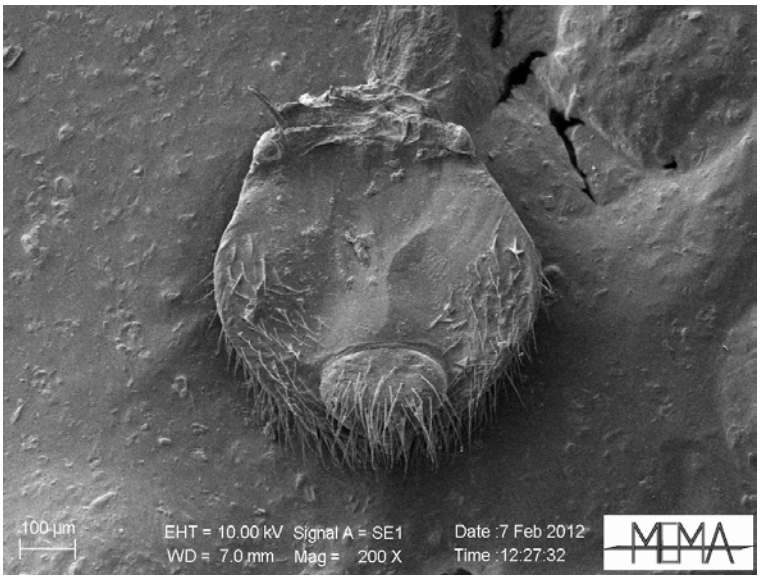

Fig. 6. Female 9th tergite of *Velia gridellii* Tamanini, 1947.

The distinction of males of *V. gridellii* is more dificult. Differences can be observed in the color of the distal angle of paratergites and parasternites. A light color (yellow) allows easy exclusion of *V. muelleri* and *V. rivulorum* (the latter has completely pale sternites in the entire abdomen). The specimens of the rare taxon *V. affinis filippii* Tamanini, 1947 can be excluded by the different shape of the connexival spines (blunt in *V. a. filippii*; pointed in *V. gridellii*).

Finally, for Alpine specimens, it is necessary to exclude the eventual (even if sporadic) presence of *V. caprai* and *V. saulii* through a comparison of the first tergites and of the abdominal pattern.

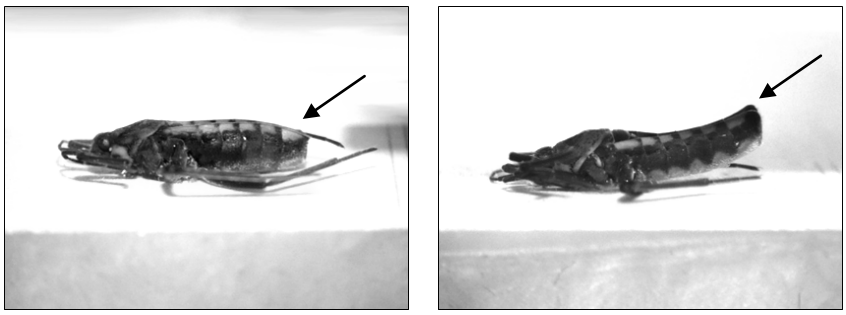

Fig. 7. Abdominal shape in the females of *Velia currens* (Fabricius, 1794) (left) and *V. gridellii* Tamanini, 1947 (right).

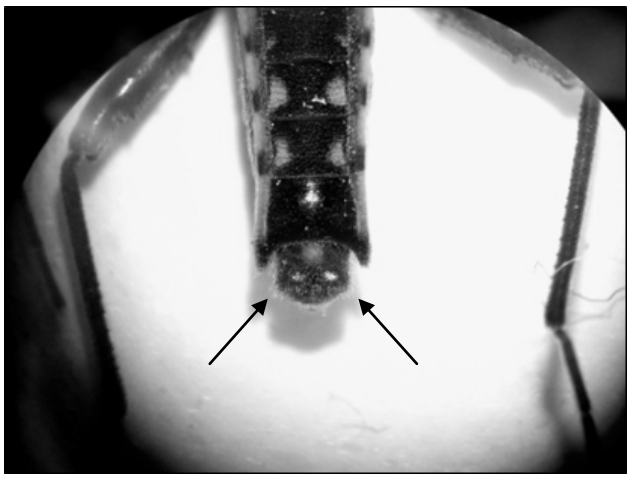

Fig. 8. Lateral edges of the 9th abdominal tergite in the male of *Velia currens* (Fabricius, 1794).

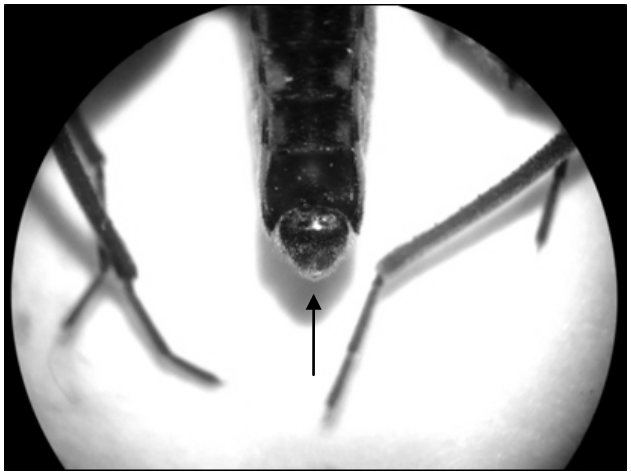

Fig. 9. Lower edge of the 9th abdominal tergite in the male of *Velia gridellii* Tamanini, 1947.

Fig. 10. Apterous male of *Velia gridellii* (photo F. Cianferoni).

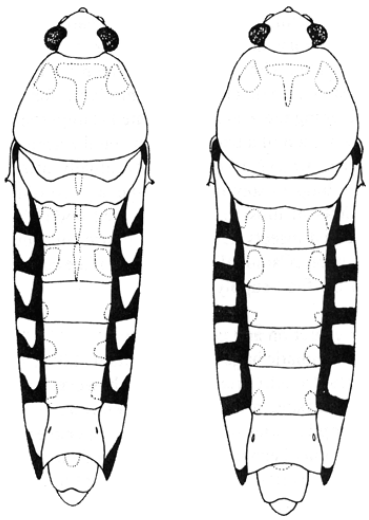

Fig. 11. Apterous males of *Velia caprai* (left) and *Velia saulii* (right). Modified from Rabitsch (2005).

Keys for the separation of *Velia currens* and *V. gridellii* from other species of the genus *Velia* in the sympatric areas.

Females (apterous and macropterous specimens)
(cylindrical abdomen; 9th tergite perpendicular to the body):

1 9th tergite trapezoidal; abodmen directed downward (Fig. 7, left) ..…….…… ***V. currens*** (Fabricius, 1794)
1' 9th tergite with rounded base; abdomen directed upwards (Fig. 7, right) ……..…….…… 2
2 1st tergite enlarged and raised (Fig. 4a); 9th tergite enlarged …….……. …… *V. muelleri* Tamanini, 1947
2' 1st tergite unraised (Fig. 4c); 9th tergite regularly rounded, not enlarged (Fig. 6); abdomen clearly directed upward, with a "saber" shape (Fig. 7, right) ……..……. ***V. gridellii*** Tamanini, 1947

Males (apterous and macropterous specimens)
(flattened abdomen; 9th tergite parallel to the body, protruding from the 8th tergite):

1 9th tergite trapezoidal (Fig. 5, left), with their lateral edges visible at the base of tergite and distinctly angular (Fig. 8) .. ***V. currens*** (Fabricius, 1794)
1' 9th tergite rounded (Fig. 5, right), protruding from the center of the base of tergite (Fig. 9) ……..…… 2
2 Abdomen laterally completely pale, also next to the thorax ……..…… ……...…… *V. rivulorum* (Fabricius, 1775)
2' Abdomen laterally from pale to dark, with darkened marking positioned almost centrally next to the thorax ……..…… 3
3 Distal angle of paratergites and parasternites pale; 1st tergite raised ……..... …… *V. muelleri* Tamanini, 1947
3' Distal angle of paratergites and parasternites dark, 1st tergite unraised ….. 4
4 Connexival spines (7th connexivum) blunt …….…… …… *V. affinis filippii* Tamanini, 1947
4' Connexival spines (7th connexivum) pointed ……..…… 5
5 First tergites (apterous morph) or abdominal pattern as in in Fig. 10 …… ……..……..…….…… ***V. gridellii*** Tamanini, 1947
5' First tergites (apterous morph) or abdominal pattern as in in Fig. 11 …… ……. *V. caprai* Tamanini, 1947 / *V. saulii* Tamanini 1947

Discussion

Velia currens and *V. gridellii* are two valid and taxonomically well defined species which can be separated mainly by the shape and structure of the male genitalia. The parameres and the endosomal sclerites must be taken in consideration for a comparison with other W-Palaearctic species. Females are easily recognizable due to several external characters: e.g. the shape of the 9th abdominal tergite or the general structure of the abdomen. These characters allow for an immediate separation even in the field, using a simple 20X lens.

On the contrary the habitus of the males of the two species is apparently more similar, and for a correct identification in the field the examination of further details (even if visible with a 20X lens) is necessary.

The field identification of the two species for ethological or ecological studies (cf. Cianferoni and Santini, 2012) is simplified by the rarity of other *Velia* spp. in large part of the distributional ranges of *V. currens* and *V. gridellii*, by species-specific "schools" and by a balanced sex-ratio (that allow to easily check both male and female specimens).

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4.2 Species groups and biogeography

Species groups and biogeographical observations in *Velia* subg. *Plesiovelia* Tamanini, 1955, with reference to *V. currens* (Fabricius, 1794) and *V. gridellii* Tamanini, 1947 (Hemiptera: Heteroptera: Veliidae)

Introduction

Velia subg. *Plesiovelia* Tamanini, 1955 belongs to the subfamily Veliinae, that contains about 130 species worldwide. Following Andersen (1981, 1982, 2000), Veliinae consists of nine genera, of which six are restricted to the New World (*Oiovelia* Drake and Maldonado-Capriles, 1952, *Paravelia* Breddin, 1898, *Platyvelia* Polhemus and Polhemus, 1993, *Steinovelia* Polhemus and Polhemus, 1993, *Stridulivelia* Hungerford, 1929, and *Veloidea* Gould, 1934); many New World species were originally placed in *Velia* Latreille, 1804. Of the three Old World genera, two (*Angilia* Stål, 1865 and *Angilovelia* Andersen, 1981) have a strictly tropical distribution in the Ethiopian and Oriental Realms eastwards to Sulawesi. *Velia*, by contrast, is a mainly West Palaearctic element (Fig. 1). Tamanini (1955a, b) divided *Velia* into three subgenera.

- The subgenus *Velia* s.str. contains only one extant species, the West and Central Mediterranean *V. rivulorum* (Fabricius, 1775).
- The subgenus *Haldwania* Tamanini, 1955 is zoogeographically Oriental, but within that region it is restricted to temperate mountain areas in Central and Southeast Asia. Species of *Haldwania* have been found in northern India, Nepal, southern and central China, and northern Vietnam. To date this subgenus contains nine species, but recent findings suggest that if more collections are made in suitable habitats (mountain streams at high altitudes), additional species belonging to this subgenus will be discovered (Tran *et al.* 2009).
- Most of the remaining species belong to the subgenus *Plesiovelia* Tamanini, 1955, which is widely distributed in Europe, Macaronesia, northern Africa, Middle East, and Central Asia, reaching the border of the Oriental Realm in northern Pakistan and northwestern India (Andersen 1981, 1995). This subgenus contains 28 taxa with 23 species and 5 subspecies (Andersen, 1995).

Velia currens (Fabricius, 1794) and *V. gridellii* Tamanini, 1947 belong to the subgenus *Plesiovelia* Tamanini, 1955 due to the morphology of trochanters (unarmed), parameres and endosomal structures.

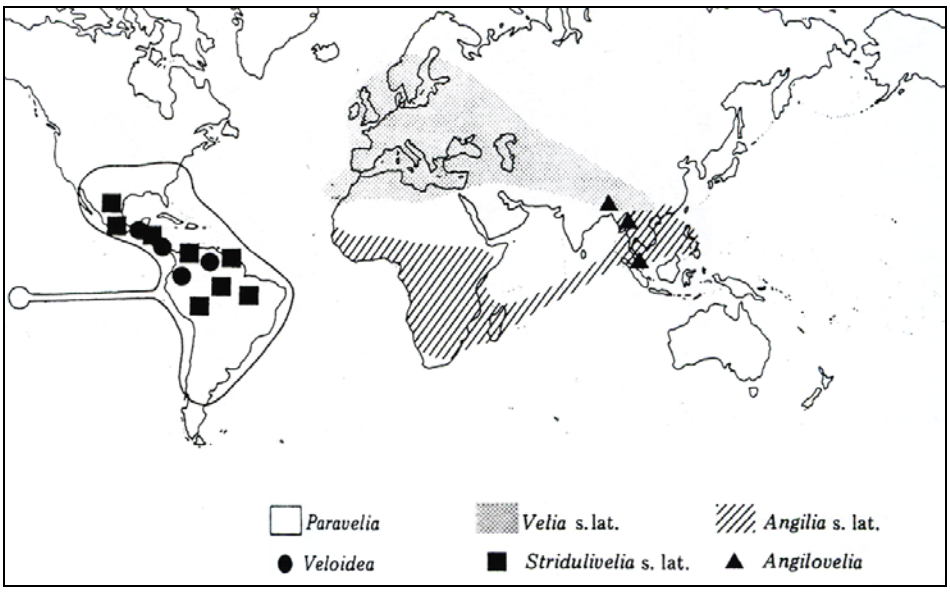

Fig. 1. Distribution of the genera of Veliinae. Modified from Andersen (1982).

Velia (*Plesiovelia*) *currens* is present from southern Calabria to the Alps (cf. Cianferoni and Terzani, under review). Its distribution extends slightly out of Italy into the French Maritime Alps and into Switzerland (Tessin), Southern Austria and Slovenia (Tamanini, 1979; Andersen, 1995; Protić, 1998).

Some recent literature quotes this species in sites outside to its present distributional range (cf. Andersen, 1995); e.g. Hufnagel et al. (1999) for Hungary or Ilie and Davideanu (2007) for Romania. This is probably due to old bibliographic references prior to Tamanini's taxonomic revision (1947) that require verification.

V. (*P.*) *gridellii* is present from southern Calabria to northern Italy and across Peninsular Italy, but its alpine range is restricted to the Prealpine arch up to the French-Italian Maritime Alps (Tamanini, 1981; cf. Bacchi and Rizzotti Vlach, 2007).

Both species are considered Italian endemics *sensu lato* (Cianferoni and Santini, 2012), because they are only present in a few istances beyond geographic Italy. However the eastern distribution of *V. currens* needs further analysis (cf. Tamanini, 1947; Gogala, 2003).

Cianferoni and Mazza (2012) connected these Alpine-Apenninic endemics (Cianferoni and Santini, 2012; Fig. 2) for the first time to main chorotypes, on the basis of the affinities amongst species groups within the subgenus *Plesiovelia*, according to the guidelines set out by Vigna Taglianti et al. (1993; 1999).

Velia currens was considered an Alpine-Apenninic endemic referred to a European chorotype, while *V. gridellii* is an Alpine-Apenninic endemic referred to a Turano-Mediterranean chorotype (Cianferoni and Mazza, 2012).

Therefore, it is possible to initially define the species groups in *Plesiovelia* Tamanini, 1955 on the basis of morphological characters.

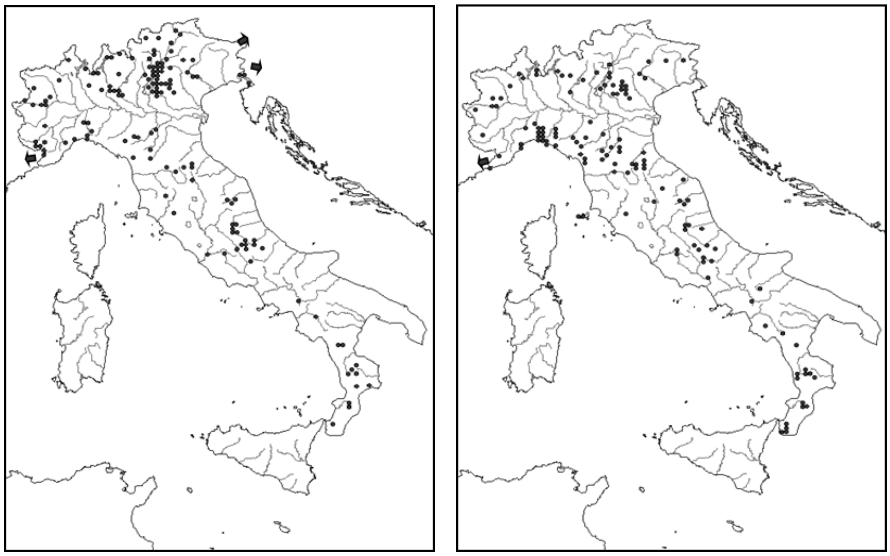

Fig. 2. Italian distribution of *Velia currens* (Fabricius, 1794) (left) and *V. gridellii* Tamanini, 1947 (right). Arrows indicate expansions out of geographic Italy. Modified from Bacchi & Rizzotti Vlach (2007).

Material and methods

According to Tamanini's studies (1946, 1947, 1949, 1951a, 1951b, 1952, 1953, 1954, 1955a, 1955b, 1955c, 1957a, 1957b, 1958, 1965, 1967, 1968, 1970, 1971a, 1971b) on *Velia* and the affinities of each taxon, I have selected some characters that can be used to separate the species of the subgenus *Plesiovelia* Tamanini, 1955 into species groups.

These characters are: the morphology of parameres; endosomal sclerites and 9th tergite for males; the abdominal shape (the last segments in particular), morphology of 7th connexivum and 9th tergite for females.

Results

On the basis of a combination of the above characters it is possible to identify two species groups within the subgenus *Plesiovelia* Tamanini, 1955:

group A (*V. currens*)

***Velia africana* Tamanini, 1946**	Maghreb
***Velia atlantica* Lindberg, 1929**	Morocco
***Velia caprai* Tamanini, 1947**	
V. caprai ssp. *caprai* Tamanini, 1947	Europe
V. caprai ssp. *bertrandi* Tamanini, 1957	Iberian Peninsula
***Velia concii* Tamanini, 1947**	Maghreb
***Velia currens* (Fabricius, 1794)**	Italy
***Velia eckerleini* Tamanini, 1967**	Maghreb
***Velia hoberlandti* Tamanini, 1951**	Iberian Peninsula
***Velia ioannis* Tamanini, 1971**	Maghreb
***Velia lindbergi* Tamanini, 1954**	Canary Islands
***Velia maderensis* Noualhier, 1897**	Maderia Island
***Velia mariae* Tamanini, 1971**	Anatolia
***Velia noualhieri* Puton, 1889**	
V. noualhieri ssp. *noualhieri* Puton, 1889	Maghreb
V. noualhieri ssp. *iberica* Tamanini, 1968	Spain and Morocco
***Velia sarda* Tamanini, 1947**	Sardinia and Corsica
***Velia saulii* Tamanini, 1947**	Europe

group B (*V. affinis*)

***Velia affinis* Kolenati, 1857**	
V. affinis ssp. *affinis* Kolenati, 1857	Near and Middle East
V. affinis ssp. *filippii* Tamanini, 1947	E-Europe
V. affinis ssp. *marussii* Tamanini, 1957	Central S-Asia
***Velia gridellii* Tamanini, 1947**	Italy
***Velia kiritshenkoi* Tamanini, 1958**	Transcaucasia
***Velia mancinii* Tamanini, 1947**	
V. mancinii ssp. *mancinii* Tamanini, 1947	E-Europe
V. mancinii ssp. *lyciae* Tamanini, 1955	Near and Middle East
***Velia muelleri* Tamanini, 1947**	SE-Europe
***Velia pelagonensis* Hoberlandt, 1941**	SE-Europe
***Velia rhadamantha* Hoberlandt, 1941**	
V. rhadamantha ssp. *rhadamantha* Hoberlandt, 1941	SE-Europe
V. rhadamantha ssp. *cyrenaica* Tamanini, 1947	Libya
***Velia serbica* Tamanini, 1951**	SE-Europe

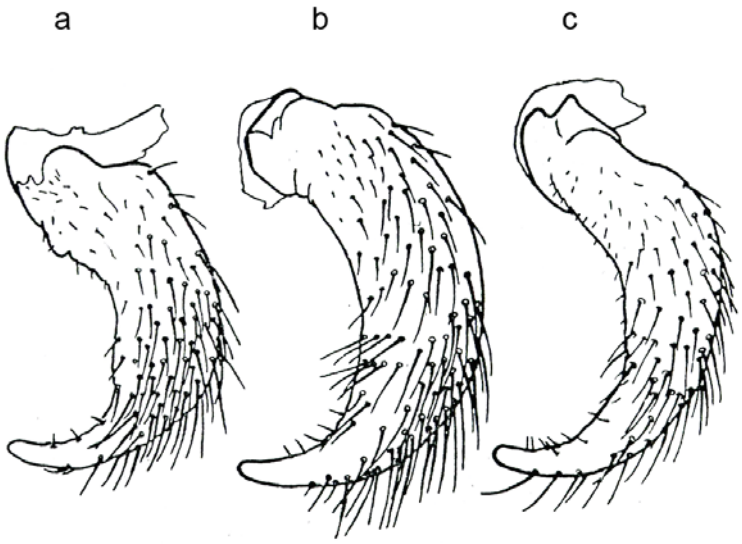

Fig. 3. Example of parameres of species belonging to the *Velia affinis* species group. a) *Velia muelleri* Tamanini, 1947; b) *V. gridellii* Tamanini, 1947; *V. pelagonensis* Hoberlandt, 1941. Modified from Tamanini (1947).

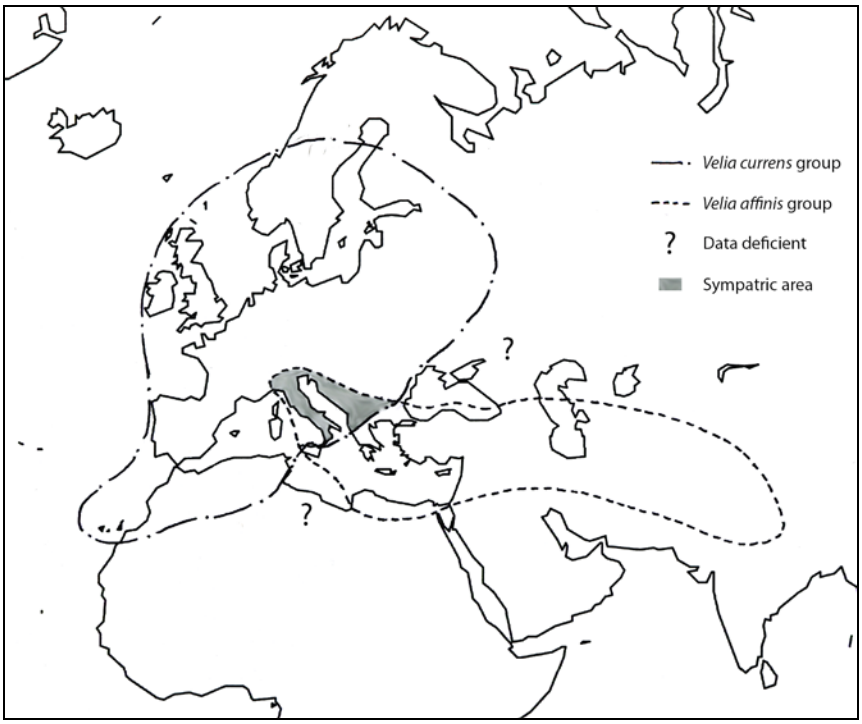

Fig. 4. *Plesiovelia* Tamanini, 1947 species groups distribution. In grey the sympatric area among species belonging to the two groups. Original.

Discussion

From an analysis of the morphological characters (e.g. Figs 3 and 5) of species belonging to the subgenus *Plesiovelia*, it is possible to identify a group of W-Paleartic species closely related to *Velia currens* (group A) and a group of eastern species (mainly E-Europeo-Asiatic) next to *Velia affinis* Kolenati, 1857 (group B), with *V. gridellii* being the most western of the species.

A sympatric area, from the Italian Peninsula to the Balkan one, exists among the species belonging to the two groups (Fig. 4). In Italy the most common species in the sympatric area are *V. currens* (gr. A) and *V. gridellii* (gr. B). Other species in the same territory are *V. caprai* and *V. saulii* (gr. A) which can coexist with *V. gridellii* (gr. B) where they pass Alps (in NE-Italy and NW-Italy); *V. concii*, known from Sicily by few specimens collected at the beginning of the 19th century (maybe extinct in Italy), could coexist with *V. muelleri* on the island (gr. B).

Concerning group B, *V. muelleri* seems to be rarely sympatric with *V. currens* (gr. A) in Southern Italy and in Central Italy, and also *V. affinis filippii* (collected few times in Italy) could seldom coexist with *V. currens* (gr. A) in Southern Italy (cf. Bacchi and Rizzotti Vlach, 2007).

This separation by species groups could help to explain the sympatry of the taxa apparently occupying the same ecological niches, as *Velia currens* and *V. gridellii* do in Italy. These species may have settled in the same territories only secondarily. The ecological differences given by Tamanini (1981), with *V. gridellii* being less sciaphilic than *Velia currens*, were in fact not confirmed by the study of Cianferoni and Santini (2012).

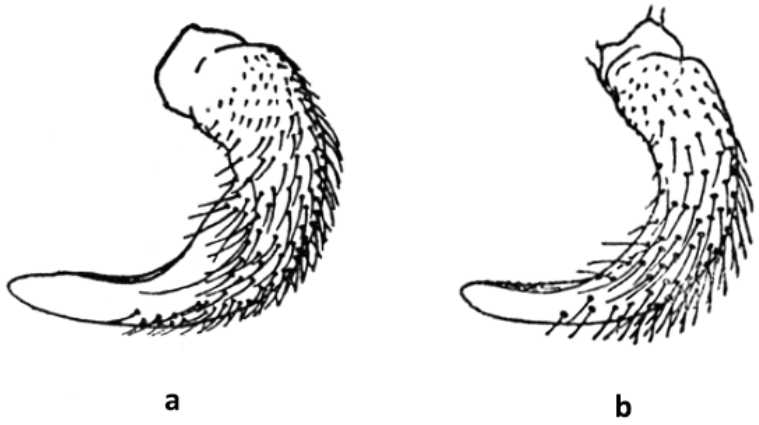

Fig. 5. Morphology of the parameres of: a) *Velia currens* (Fabricius, 1794) and b) *V. saulii* Tamanini, 1947. Modified from Rabitsch (2005). Several analogies in their morphology lead to consider *V. currens* as a geographical vicariant of the European species *V. saulii*, maybe splitted by the Alpine barrier.

Finally, it is important to point out that these preliminary observations are exclusively based on morphological affinities, and that further studies with genetic markers will be necessary in order to verify the monophily of the groups and the existence of two different centres of origin.

The observed low co-occurrence of *Velia currens* and *V. gridellii* (Cianferoni and Santini, 2012), despite the sympatry over a large part of their distributional ranges, suggests the possibility of competiton between the two taxa. This hypotesis would seem to be supported by the larger size, on average, of *V. gridellii* (cf. Tamanini, 1947) and by preliminary observations like the exclusive finding of this species in sites previously occupied only by *V. currens* (pers. obs.).

Acknowledgements

My sincerest thanks go to Luca Bartolozzi (Natural History Museum of the University of Florence, MZUF) for the review of the manuscript, to Fabio Terzani, Filippo Ceccolini (MZUF) and Giuseppe Mazza (Dpt. of Evolutionary Biology, University of Florence) for their precious advice, and to Juliet Strachan (Florence, Italy) for the English revision.

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4.3 Life histories, wing polymorphism and co-occurence

Ecology and life histories of two Alpine-Apenninic species of *Velia* (Hemiptera: Heteroptera: Veliidae)

Abstract. *Velia currens* (Fabricius, 1794) and *V. gridellii* Tamanini, 1947 are two South European species of Veliidae, whose ecology and behaviour are poorly known. The aims of this study were to investigate their life histories, quantify occurrence of wing polymorphism and gather information on their degree of co-occurrence. Nine different populations were regularly surveyed from April to November 2010. Furthermore, a dataset containing information on the occurrence of the two species and the presence of winged morphs at 294 sites was compiled from museum collections, private collections and published literature. No evidence for multivoltinism was detected in either species. However, oviposition and and/or hatching were protracted in time so that early-instar nymphs and adults co-occurred up to midsummer. Although their distributional ranges completely overlap at a large spatial scale, the two species co-occurred only rarely at the same sites and the degree of co-occurrence was lower than expected by chance. Winged specimens were rarely recorded. At least in *V. gridellii*, the numbers of winged individuals were inversely related to the altitudes of the sites. During the summer, when some of the streams surveyed dried up, several specimens were found in an apparent state of lethargy, under stones. It is hypothesized that the ability to aestivate, coupled with the ability to walk from one site to another may reduce the advantage associated with producing winged forms and account for the low rate of occurrence of macropterism in these species.

Introduction

Semi-aquatic bugs (Hemiptera: Heteroptera: Gerromorpha) have highly diverse life cycles and life histories, a feature that has attracted numerous studies in the past (see e.g. Andersen, 1982; Ditrich and Papáček, 2009a, c). Gerromorpha are recorded to be both uni- and polyvoltine (Andersen, 1982). In temperate areas some species are strictly univoltine (e.g., some *Gerris* spp.: Mitis, 1937; Brinkhurst, 1959; Vepsäläinen, 1974) or multivoltine (e.g., some *Microvelia* spp.: Tamanini, 1979; Ditrich and Papáček, 2009c), but several species may be either uni- or polyvoltine, depending on environmental conditions (e.g. temperature or photoperiod: Vepsäläinen, 1974). If multivoltine, up to three generations have been hypothesized (e.g. Ditrich and Papáček, 2009c).

A particular feature of the life history of Gerromorpha is wing polymorphism, which consists of the simultaneous occurrence, within the same species, of two or more phenotypes (morphs) that differ in terms of the development of their flight apparatus (Andersen, 1982). Although this phenomenon is documented for several species of Gerromorpha (e.g. Brinkhurst, 1959; Andersen, 1973, 1982, 1993; Vepsäläinen, 1973, 1974, 1978a) it is still not fully understood and several possible determinants are proposed in the literature. Although it is postulated that the development of winged morphs is genetically controlled (e.g. Spence and Andersen, 1994), the occurrence of this morph is known to depend upon environmental factors, such as photoperiod and temperature (e.g. Muraji et al., 1989; Spence, 1984; Pfenning et al., 2008). In addition, the incidence of winged morphs is usually associated with different degrees of habitat stability (see Andersen, 1993; Ditrich and Papáček, 2009b and references therein). The observation that the frequency of winged specimens tends to increase as habitats become less predictable in both space and time led to the idea that winged individuals enable species to disperse in patchy/unstable habitats (Brinkhurst, 1959; Socha and Zemek, 2003). Other factors, including population density and food availability, are also thought to affect the induction of winged forms (e.g. Muraji and Nakasuji, 1988; Muraji et al., 1989; Harada et al., 1997; Pfenning et al., 2007; Ditrich and Papáček, 2010b).

Among the West Palaearctic Gerromorpha, the most widely studied family, both in terms of life histories and wing polymorphism, is Gerridae (see Spence and Andersen, 1994 and Ditrich and Papáček, 2009a for reviews), whereas other families, such as Veliidae, received less attention until recently (Ditrich et al., 2008, 2011; Ditrich and Papáček, 2009a, b, 2010a, b; Ditrich and Koštál, 2011). Furthermore, most of the available information on Veliidae, refers to species in Northern and Central Europe (e.g. Mielewczyk, 1980; Murray and Giller, 1991), while little or nothing is known about more southern taxa.

TABLE 1. Major environmental features of the nine sites sampled. "Water permanence" indicates whether during the study period a stream completely ran dry (temporary) or not (permanent). "Streambed" and "Banks" indicate the dominant type of substrate at the bottom and on the banks of a stream, respectively. "Sun exposure" indicates whether a site was exposed to direct sunlight (sun) or not (shadow), for most of the day. "Habitat" is the type of environment surrounding each site sampled. Average water and air temperatures recorded during the study period are also provided, together with their minimum and maximum values.

Code	Geogr. coordinates UTM WGS84 (East North)	Altitude (m)	Width (m)	Depth (cm)	Water permanence	Streambed	Banks	Sun exposure	Habitat	Temperature water (°C)	Temperature air (°C)
L1	685920 4850715	90	2.0	60	temporary	pebbles	mud	sun	field	17.0 (11.5–22.0)	21.5 (11.0–30.5)
L2	695420 4848065	110	3.0	30	permanent	pebbles	grass	sun	field	15.0 (11.5–17.0)	23.0 (13.5–32.0)
L3	695300 4847925	110	3.0	40	permanent	sand	mud	shadow	wood	16.0 (13.0–19.0)	19.5 (13.0–24.0)
M1	683390 4863035	290	8.0	40	temporary	pebbles	grass	shadow	wood	17.5 (13.0–23.0)	20.5 (12.5–24.0)
M2	682960 4862865	290	4.0	20	temporary	pebbles	mud	sun	wood	15.5 (12.0–19.0)	24.5 (12.5–24.5)
M3	682570 4866960	290	5.0	50	permanent	sand	mud	sun	wood	15.0 (12.0–17.0)	20.5 (10.5–28.0)
H1	689130 4860965	555	2.0	10	permanent	pebbles	mud	shadow	wood	12.5 (10.5–14.0)	17.0 (11.0–23.0)
H2	686930 4862065	585	1.5	50	temporary	pebbles	rocks	sun	wood	13.5 (9.0–18.0)	16.0 (11.0–21.0)
H3	689770 4861065	615	3.0	15	permanent	pebbles	mud	shadow	wood	12.0 (9.0–14.5)	18.5 (11.0–24.5)

For example, the data available in the literature on wing polymorphism in the genus *Velia* are almost exclusively for the centralnorthern European species *Velia caprai* Tamanini,1947 (e.g. Brinkhurst, 1959; Ditrich and Papáček, 2009b).

The present paper reports an analysis of the biology of two southern species of the genus *Velia* Latreille, 1804, subgenus *Plesiovelia* Tamanini, 1955, in central Italy (Tuscany): *Velia currens* (Fabricius, 1794) and *V. gridellii* Tamanini, 1947. Tamanini (1979), in his comprehensive monograph of Italian Gerromorpha and Nepomorpha, reports that all species of *Velia* are univoltine, but this may not be case. For example, although the congeneric *Velia caprai* is predominantly univoltine (Brinkhurst, 1959), a second summer generation is occasionally produced, at least in the warmer areas of its range (e.g. Mielewczyk, 1980; Papáček and Jandová, 2003). There are no specific studies on the two species analysed in the present work. Similarly, although it is claimed that all species of *Velia* belonging to the subgenus *Plesiovelia* are dimorphic, with both apterous and macropterous forms (Andersen, 1982), there is no quantitative data available on the two species studied.

There were three main aims to this study. First, to describe, using repeated surveys of nine populations, the life histories of the two species. The populations surveyed were in streams representative of the full range of types of streams inhabited by the species. In particular, the intention was to asses if the two species were uni- or multivoltine and how the time of emergence of adults and nymphs changed with altitude. The second aim was to obtain quantitative information on the occurrence of wing polymorphism, and finally, the degree of co-occurrence of the two species. The work combined direct surveys of natural populations with the construction and analysis of a large database of information on the distribution, occurrence and incidence of wing polymorphism in the two species.

Material and methods

Species and study sites

The species studied were *Velia* (*Plesiovelia*) *currens* (Fabricius,1794) and *V.* (*P.*) *gridellii* Tamanini, 1947. These species are Alpine-Apenninic elements, belonging to the S-European chorotype (Vigna Taglianti et al., 1993, 1999) and though their distributions extend slightly into the French Maritime Alps (both *V. gridellii* and *V. currens*) and that of *V. currens* into Switzerland (Tessin), Southern Austria and Slovenia (Tamanini, 1979; Andersen, 1995; Protić, 1998), they can be considered to be Italian endemics sensu lato. Both species are typical inhabitants of the surface of streams, and as altitude and associated habitat stability (perennial or seasonal) are claimed as possible determinants of the occurrence of wing polymorphism, the streams selected were located at different altitudes. Specifically, three altitudes were chosen: (a) a low altitude (L), corresponding to ~100 m amsl; (b) medium altitude (M),

corresponding to ~300 m amsl; and (c) high altitude, at about 600 m amsl. Three replicated streams were sampled at each altitude ($\Sigma n = 9$) and all are located in the Province of Florence (Tuscany; Italy). For each stream, the following were recorded: (i) water and air temperature (°C), measured during each survey; (ii) water permanence (temporary, if the site dried up during a survey; permanent, if not). A complete list of the sites sampled together with their major environmental features is provided in Table 1.

Streams were sampled regularly at 15-day intervals from April to September 2010, with monthly samples taken in October and November 2010 on sunny, calm days. At each sampling site (stream) a transect 10 m long was established at random. Two different sampling protocols were followed to investigate life histories and wing polymorphism. For lifehistory reconstruction, all specimens (adults + nymphs) collected during a 30-min survey along each transect were examined. Animals were captured in order to identify them and avoid double counting. More time was spent sampling when some of the streams dried up and no swimming specimens were visible. In these cases, dried out sections of the streams were systematically searched for specimens hidden under stones. To quantify the occurrence of wing polymorphism, the sites were sampled until 50 adults or IV/V-instar nymphs were captured. Unambiguously discriminating the presence of wing pads to infer the morph of the earlier stages was difficult and so these stages were not included in the sample. Identification took place directly in the field, using a portable 20X lens. All the specimens were released where they were collected at the end of the day. Species/stage identification was carried out as follows. Firstly, adult specimens of other coexisting *Velia* species [i.e. *V. muelleri* Tamanini, 1947 and *V. rivulorum* (Fabricius, 1775)] were excluded from the samples. Then, *V. currens* and *V. gridellii* were identified based on the shape of the abdomen in lateral view (adult females) and 9th tergite (adult males), in accordance with Tamanini (1947, 1979). The identification of the nymphs was based on the length of legs and antennae, and head width (López et al., 1998; Ditrich and Papáček, 2010b). A reference box with several specimens of all instars belonging to the two species identified in laboratory was also taken into the field for comparison.

Database preparation

A database comprising previous observations on the two species was created. This was based on lists of specimens preserved in museum and private collections, data previously obtained by the first author and records in the literature. Collections used to create the database were: the Natural History Museum of the University of Florence, Zoological Section (MZUF), the Natural History Museum of Milan (MSNM); the private collections of F. Cianferoni (Florence), J. Damgaard (Copenhagen), A. Mascagni (Florence) and F. Terzani (care of MZUF).

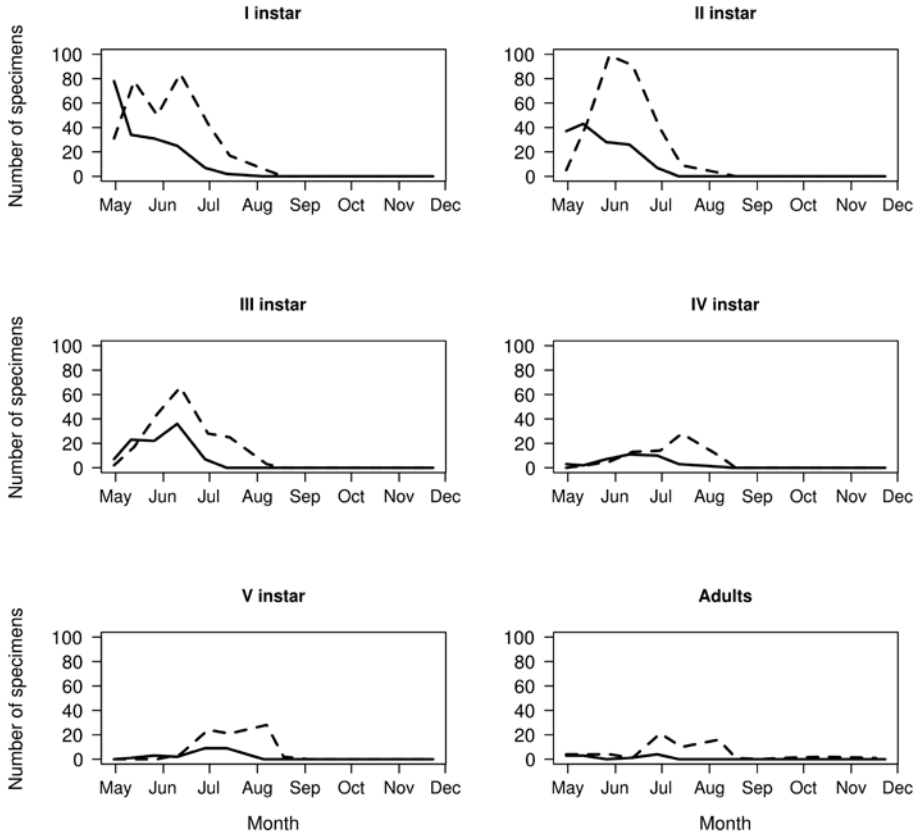

Fig. 1. The numbers of *V. currens* (nymphs and adults) recorded during the study period. Sites L2–L3 – continuous line; Sites M1–M3 – dashed lines.

Other data were obtained from Tamanini (1947) and Dionisi (2007). Only records for which it was possible to unambiguously locate the sampling site were considered. Each database entry included a record of the locality collected, date, species, number, sex and development of the wings (apterous/ macropterous) of the specimens. A total of 294 sites were recorded in the database, covering almost all Italian regions where the two species are present, although the majority came from Central Italy. Some records from South Eastern France were also present. For each site only the presence/absence of macropterous specimens was considered, as information on their abundance was irregular and unreliable. The presence of winged specimens at each site was modelled using logistic regression (Zuur et al., 2009) with altitude (Alt) as the explanatory variable. The statistical significance of this model was determined by comparing (likelihood-ratio test) it with a model not including the factor Alt (intercept-only model). Differences in average altitude of sites where the two

species were found (apterous and macropterous specimens pooled), were tested using Welch t-test after square-root transform of data to achieve normality of data (Sokal and Rohlf, 1995).

To assess co-occurrence patterns between the two species a null-model analysis was performed (Gotelli, 2000). Observed co-occurrence (OCO) was computed as the number of sites where both species were found. Taking "Ngrid" and "Ncurr" as the number of occurrences of *V. gridellii* and *V. currens*, respectively, in the database, 50000 surrogate datasets were randomly generated, each containing Ngrid and Ncurr occurrences of the two species. The co-occurrence (SCO) of these two species in each of the simulated datasets was computed. If co-occurrence of the two species is random, the OCO value is expected to equal the average SCO, however, if the two species co-occur less frequently than expected by chance, an OCO less than the average SCO is expected. The null hypothesis that OCO = SCO was tested counting the number of SCO values less than or equal to OCO (Gotelli, 2000).

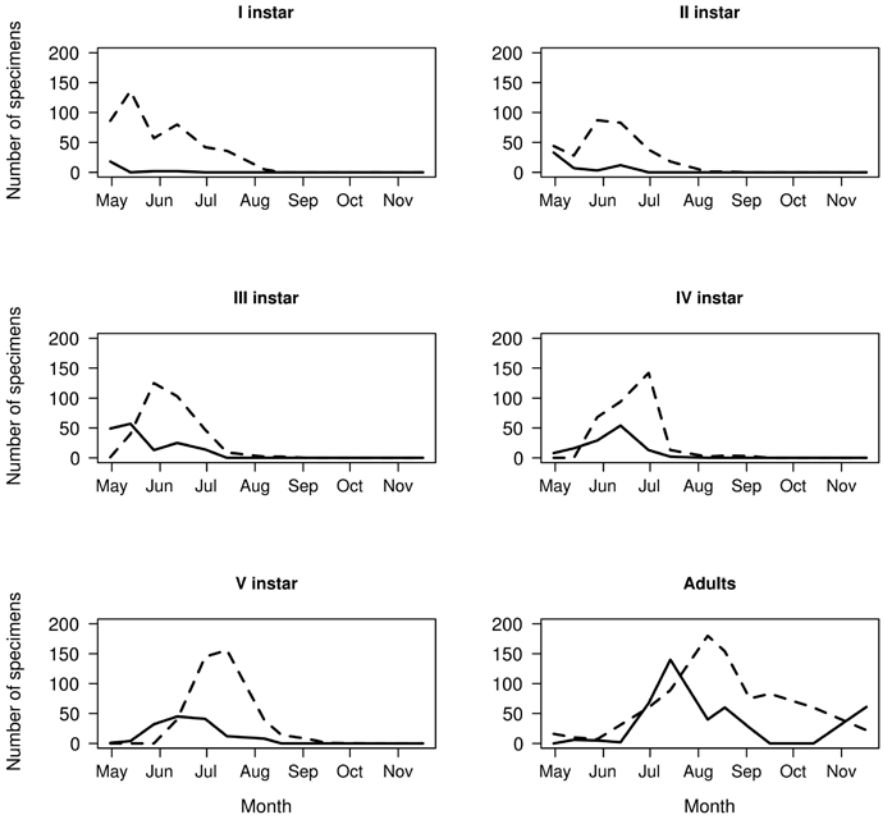

Fig. 2. The numbers of *V. gridellii* (nymphs and adults) recorded during the study period. Site L1 – continuous line; Sites H1–H3 – dashed lines.

All the analyses were carried out using the R (ver. 2.13.1) software package (R Development Core Team, 2011).

Results

A total of 1568 specimens (adults + nymphs) of *V. currens* and 3601 of *V. gridellii* were observed during this study, but little co-occurrence between the two species was detected. *V. currens* was detected at low (sites L2–L3) and medium altitudes (M1–M3), but not at the highest sites. In contrast, *V. gridellii* was found at the highest sites (H1–H3) and at only one of the lower sites (L1). A few specimens of *V. gridellii* were occasionally found at sites L3 and M3 and were not included in subsequent analyses. The numbers of specimen retrieval during the sampling period of the study are shown in Figs 1 and 2 for *V. currens* and *V. gridellii*, respectively. The developmental cycles of the two species also differed in other aspects. In particular, in *V. currens* high numbers of first instar nymphs were followed by progressively lower numbers of later stages (Fig. 1). At medium altitudes, for example, nymph numbers reached a maximum value of 99 (II instar), while the peak for adults never exceeded 21 specimens (Fig. 1). Numbers at lower sites were even lower. This pattern of adult loss was less evident in *V. gridellii*, for which equal or even higher numbers of adults than nymphs were observed (Fig. 2). Within each species, the life histories showed a broad dependence upon altitude, with peaks in abundance of the different stages generally occurring earlier at lower altitudes. The number of individuals observed during the different sampling periods suggests that both species are univoltine. At each site, in fact, for each stage only one developmental peak was observed.

One stream at each altitude ran dry from the end of July to September (Table 1). During this period, a total of 10 *V. currens* (6 males, 4 females) and 94 *V. gridellii* (47 males, 47 females) specimens were found hidden under stones in the beds of the dried out streams, seemingly in a state of lethargy: they were inactive and did not react initially to mechanical stimuli. Stimulation, which included manipulation for collection, identification and exposure to light lasted about 30 s. All the specimens reverted to a state of activity after a few tens of seconds or minutes. No macropterous specimens were found among the 3000 individuals (350 *V. currens* and 2650 *V. gridellii*) sampled during the field surveys at the nine study sites and analysis of the database confirmed that macropterous forms occur at very low frequencies. Macropterous specimens of *V. gridellii* were recorded at only 11 out of 192 sites (four males, six females and one V-instar nymph). Similar numbers were found for *V. currens*, with a total of six males and 10 females found at 10 out of 138 sites. The frequency of macropterous occurrence in the two species was not statistically different (χ^2 = 0.108, df = 1, P = 0.7427). Furthermore, no evidence of a biased sex ratio was found in macropterous specimens: chi-square test results for a different-from-equal sex ratio were P = 0.55 and P = 0.32 for *V. currens* and *V. gridellii*, respectively.

A significant negative relationship between the occurrence of macropterous specimens and site altitude was detected by regression analysis only for *V. gridellii* (Fig. 3). In fact, the model including altitude performed better than the intercept-only model (likelihood-ratio test = –8.4004, P 0.005). The predicted probability of finding macropterous specimens is at a maximum (~0.18) at low altitudes and then declines rapidly as site altitude increases, becoming almost equal to 0.05 at 500 m. For *V. currens* however, there was no significant relationship between the occurrence of macropterous specimens and altitude. The model including altitude was in fact indistinguishable from the intercept-only model (likelihood-ratio test = –2.5442, P > 0.1). On average, *V. currens* (all specimens pooled) occurred at slightly lower altitude sites (mean altitude = 452 m, with 509 and 400 m being their upper and lower 95% CI) than *V. gridellii* (mean altitude = 526 m, with 585 and 470 upper and lower 95% CI) although this difference was not statistically significant (Welch t-test = –1.8081, df = 316.30, P > 0.07).

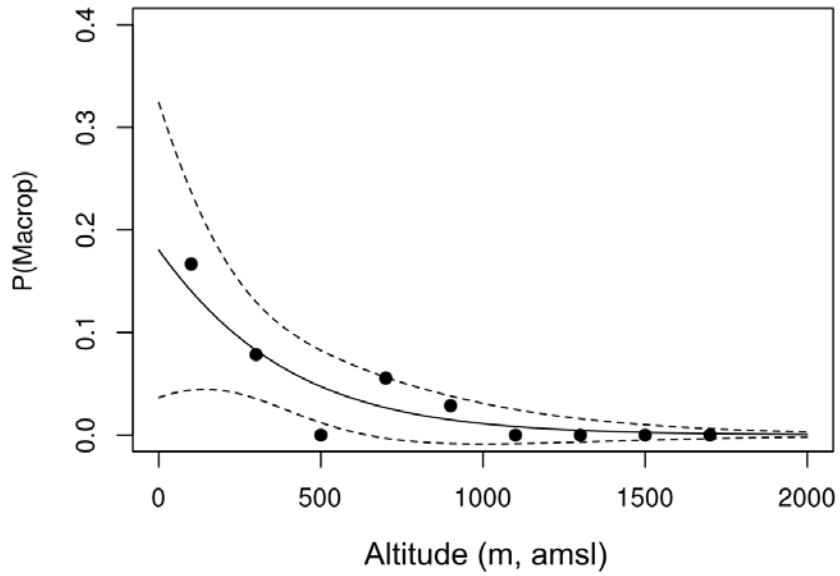

Fig. 3. Probability of recording macropterous individuals P(Macrop) of *V. gridellii* at sites situated at range of different altitudes. The solid line represents the estimated relationship and the dashed lines the 95% confidence intervals. Dots represent the observed frequency of macropterous individuals and are the averages for sites in 200 m ranges in altitude from 100 to 1700 m.

Based on the evidence from the database, the two species co-occurred less frequently than expected by chance. The observed co-occurrence (OCO) was in fact only 25 (out of 294 sites), which is approximately half of the mean simulated value (SCO = 53.05 ± 4.84 SE). The null hypothesis that OCO = SCO could safely be rejected since only 14 of the 50000 simulated SCOs were less than or equal to OCO, giving P = 0.00028.

Discussion

The results of this study showed no clear evidence of multivoltinism in either of the two species. Generally there was only one peak in numbers in each of the life stages (I–V-instar nymphs and adults), with the only exception being *V. gridellii* at the lower altitude sites. This finding agrees with previous observations by Tamanini (1947, 1979), who claimed that univoltinism may be the norm for all *Velia* species in northern Italy, although the possibility that different generations may coexist in more southern populations was not excluded. However, if these two species are not multivoltine then the laying and/or hatching of their eggs must have occurred over a long period of time as early-instar nymphs and adults co-occurred over much of the period of this study. First-instar nymphs, for instance, were observed up to mid July, when the peak number of mature adults occurred. However, it cannot be completely ruled out that these late nymphs belonged to a second generation mixed with the previous one (e.g. Murray and Giller, 1991; Ditrich and Papáček, 2009c). The second autumn peak observed in *V. gridellii* is unlikely to have been due to the production of a second generation as it was not preceded by a similar pattern in nymph abundance. In fact, this peak appeared after the summer reduction in activity, when most of the streams dried up and is, therefore, likely to be related to the resumption of activity of previously aestivating adults. This point will be further discussed below. In this study, sampling started during spring and no information was collected on the behaviour of this species during the winter. A further development of this study should thus focus more closely on this subject. In particular, it is important to check whether females in autumn and/or spring contain chorionated eggs, which would indicate the overwintering of reproductive females and the possibility overwintering in both the egg and adult stages. This way of overwintering, detected in *V. caprai* and *V. saulii* (see Ditrich and Koštál, 2011), seems to be a crucial aspect of the distribution of these species in northern regions, verifying its occurrence in Mediterranean species of this genus would be of great interest.

Nymphal development was presumably affected by temperature: faster developmental rates were observed at low/medium altitudes, where water and air were generally warmer. This finding agrees with previous observations on the Central European species *V. caprai* (Murray and Giller, 1991; Ditrich and Papáček, 2009b), other species of gerrids (e.g. Spence and Andersen, 1994; Pfenning and Poethke, 2006) and more generally what is known regarding insect development (e.g. Chown and Nicolson, 2004). Caution must be

exercised, however, as temperature is only one of the possible factors affecting nymphal development that changes with altitude; other possibilities might be population density and/or prey availability (Bronmark et al., 1985; Blanckenhorn, 2006; Ditrich and Papáček, 2010b). Due to the different altitudinal distributions of the two species, it is difficult to separate species differences from those induced by environmental factors.

In *V. currens*, high numbers of first instar nymphs were followed by progressively lower numbers of later stages, a pattern broadly expected due to natural mortality during the different stages. A different pattern however, was observed in *V. gridellii*, where equal or even higher numbers of adults than nymphs were observed. The reasons for this unexpected pattern are not yet known but there are two plausible explanations. It is possible that there is an influx of adult specimens from upper sections of the same streams (Ditrich and Papáček, 2009b). This point is consistent with the fact that this pattern was more pronounced in the lower stream where this species was found. Sampling error (e.g. due to the lower mobility and catchability of nymphs than adults) as a cause however cannot be completely ruled out.

The differences in altitude at which the two species were found constitute an important discussion point. In our field samples *V. gridellii* occupied higher altitudes than *V. currens*. This finding not only contrasts with previous observations, showing that both species may be present irrespective of altitude (see Bacchi and Rizzotti Vlach, 2007), but also with evidence from our database, where no difference in altitudinal range was detected. The observed separation of the two species should, at least in part, be attributed to factors other than altitude, or the environmental determinants directly correlated with it, such as temperature. Altitudinal differences in the distributions of the specimens sampled are, in our opinion, most likely to be a consequence of secondary effects of a more general mechanism separating the two species. Of course, these differences may also be due to an undetected bias in the selection of sampling sites. A spatial segregation of the two species was detected by nullmodel analysis, showing that the two species co-occurred less frequently than expected by chance. However, the actual mechanism behind this pattern remains uncertain and may range from competitive exclusion, to habitatdriven segregation based on an unknown environmental factor. Inferring such effects from the observed pattern without additional data is, however, impossible at this stage (Gotelli, 2000) and may represent a further goal for future research. Whereas it is known that different species of Gerromorpha may show spatial partitioning due to differences in habitat features (see, for example, Andersen, 1982; Karaouzas and Gritzalis, 2006; Ditrich et al., 2008), no information exists on the competition among these species of aquatic Heteroptera, although competitive interactions among sympatric corixid species are documented (Vepsäläinen, 1978b). A caveat to this discussion is the reliability of the database records. Although analyses of data based on voucher specimens or databases compiled from literature sources is increasingly regarded as a useful

and sometimes fundamental tool in biodiversity research (see, for example, Schlick-Steiner et al., 2003), the reliability of collections has to be carefully checked before any firm conclusions can be drawn. The results of the analysis of co-occurrence may be trusted if it is true that both species were searched for equally, at all sites (that is to say that collectors did not selectively catch one species or the other). In fact, we are confident that this assumption was fulfilled with respect to our database. Care was taken to directly ask the owners of the personal collections for confirmation in this regard. This was also clearly stated in published material, as well as for the museum collections, for which a careful inspection of all notes, sketches and related issues was carried out.

The occurrence of macropterous specimens was very low in both species, even lower than that reported for other *Velia* species (e.g. Brinkhurst, 1959). In database samples, although winged morphs occurred with a similar frequency in both species, a significant dependency on altitude was found for *V. gridellii* but not *V. currens*. The observed altitude-related effect broadly supports the hypothesis that macropterism may be linked to environmental determinants, and presumably to those related with habitat predictability and stability. The absence of macropterous specimens in our field samples may simply be due to the low incidence of macropterism in these species. Despite the high total number of individuals observed, the number of sites visited was limited (three for each altitude level, making a total of nine) and the probability of finding a "positive" site (i.e. one with macropterous individuals) at each level was very low. Moreover collecting is usually associated with a positive bias towards rare morphs, so that the relative numbers of macropters in collections might be greater than in nature.

An important point worth noting was the presence, during summer, of adults of both sexes hidden under the stones in dried-up streams. These specimens were seemingly aestivating in a state of lethargy, as indicated by the fact that they remained completely immobile and did not initially responded to external stimuli when uncovered. Aestivation has been described before in Gerridae (Hauser, 1982) and hibernation is frequently recorded in waterbugs, including *Velia* spp. (e.g. Brinkhurst, 1959b; Murray and Giller, 1991; Ditrich and Papáček, 2009a). Aestivation probably also occurs in *V. caprai*, as firstly suggested by (Ditrich, 2005), and partly confirmed by Ditrich and Papáček (2008) and Ditrich and Koštál (2011). However, it is unclear if the aestivation observed in *Velia* spp. is really a true diapause (with arrested gonad development) or just some kind of quiescence. An ad-hoc study on the state of gonads during the summer would help to resolve this issue. The presence of adult *Velia* spp. hiding under stones in dried-up stream-beds, during summer and early autumn, has been observed by P. Štys (pers. comm.) on several Greek islands, although these adults were not lethargic. Finally, Bronmark et al. (1985) after a markrecapture study of *V. caprai* populations in Sweden conclude that only a small fraction of the populations was active at any one time, suggesting a great number of specimens remained hidden. This kind of behaviour may be

adaptive during summer droughts (Southwood, 1962) as it makes it more likely they will survive until the onset of the autumn rains that rejuvenate the streams. This was particularly evident for *V. gridellii* at the lower sites, where adults reappeared in autumn, having previously disappeared during the summer months.

It could therefore be hypothesized that the ability to aestivate may make it less advantageous to produce winged specimens and account for the low rate of occurrence of macropterism in these species. In fact, macropterous specimens, although able to travel long distances in search of a suitable environment when faced with unfavourable conditions (Andersen, 1982), generally incur a cost in terms of reduced fecundity, at least in females (see the review by Zenna and Denno, 1997), and so it is likely that a trade-off exists between the benefits (if any) of macropterism and the associated cost to reproduction. It is important to stress that the ability of macropterous specimens to fly has never been verified in this species and at present it is only possible to speculate what the possible benefits of being able to disperse by flying might be. The ability to endure unfavourable conditions by aestivating may reduce the advantage associated with producing winged forms. Furthermore, some *Velia* species can crawl out of water (e.g. Andersen, 1982), the most striking example of which is the case of *V. caprai*, as reported by Ditrich and Papáček (2009b, 2010a). They revealed using both mark-recapture in the field and laboratory experiments that this species surprisingly can walk over land for up to tens of meters. Individuals of both *V. currens* and *V. gridellii* were also occasionally observed walking short distances over land during the present study, but the maximum distance travelled was not recorded. Therefore, aestivation coupled with an ability to walk out of water may partly act as a substitute for dispersion by flight.

In conclusion, the results presented in this paper help to shed some light on the life-history traits of these two *Velia* species, for which very little is known. Details of the incidence of macropterism add to existing knowledge on this intriguing aspect of Gerromorphan biology (Andersen, 1982) and corroborate previous findings on its determinants. Furthermore, the findings on spatial segregation of the two species pose new questions about their ecology and highlight the need for further investigations to clarify the causes of such a pattern. Finally, apart from improving our understanding of the ecology and behavioural traits of these species, a better understanding of their biology may help us conserve these organisms, for which the combined effects of restricted distribution (endemic to Italy s. l.) and increasing effect of humans upon freshwater habitats (EEA, 2010) pose serious threats to their survival.

Acknowledgements

Thanks are due to F. Terzani and S. Rocchi (MZUF) for providing specimens for this work and L. Bartolozzi (MZUF) and M. Pavesi (MSNM) for allowing the first author to study museum collections. R. Dionisi (Rome, Italy) kindly provided further useful data from his own samples. Many thanks are also due to D. Samancioglu, A. Fortunati and G. Mazza (Florence, Italy) for their help during the fieldwork. We are grateful to P. Štys (Charles University, Prague, Czech Republic) and two anonymous referees, for their suggestions, which contributed to improve the manuscript.

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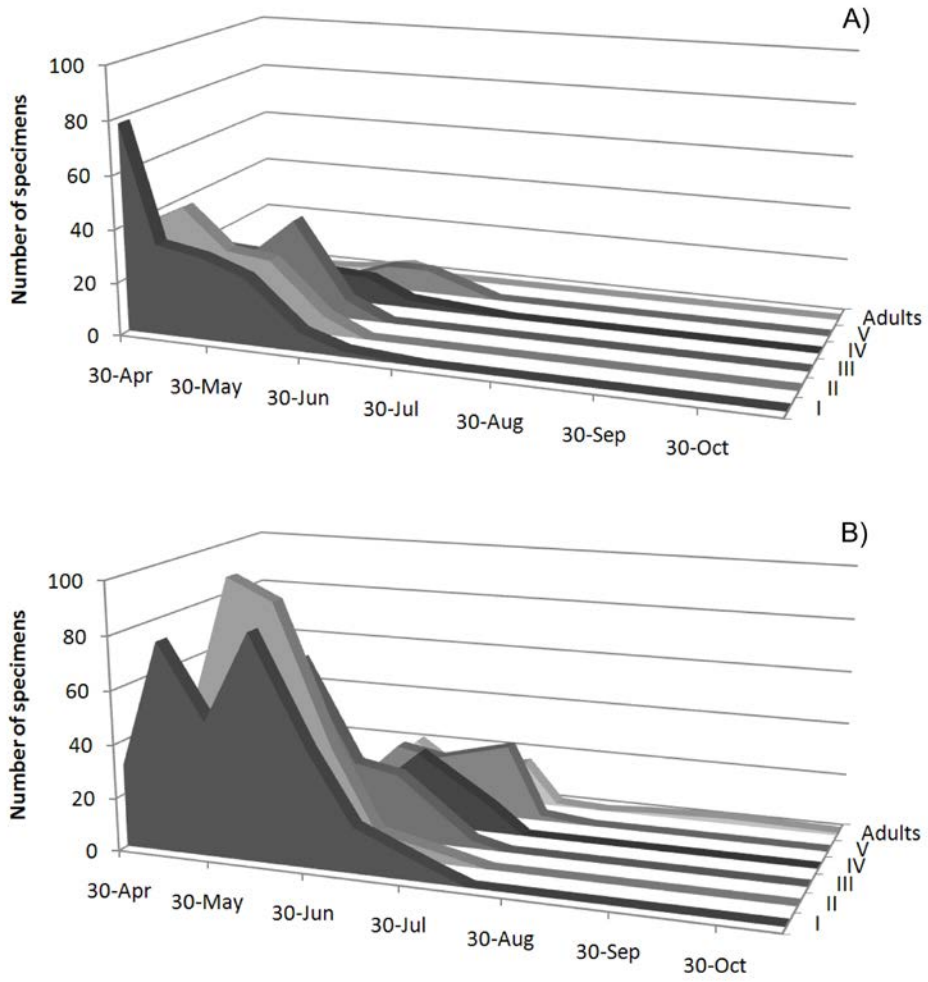
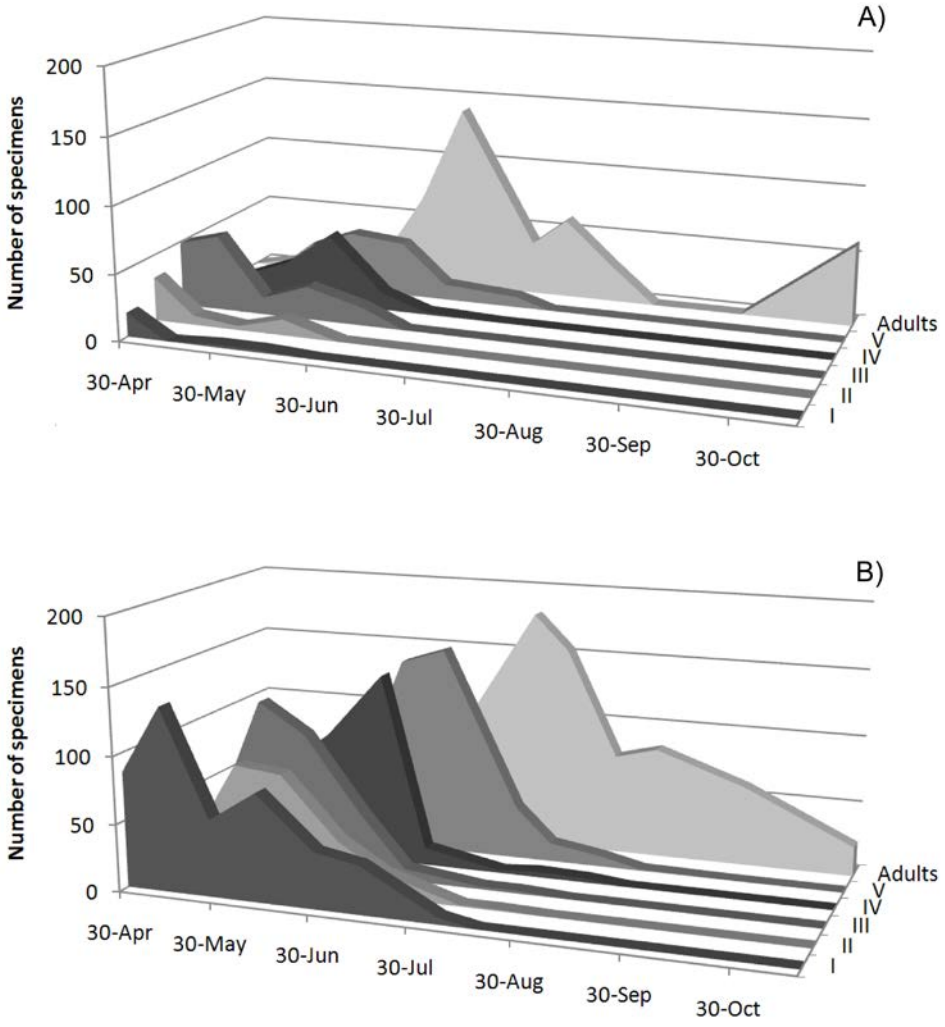
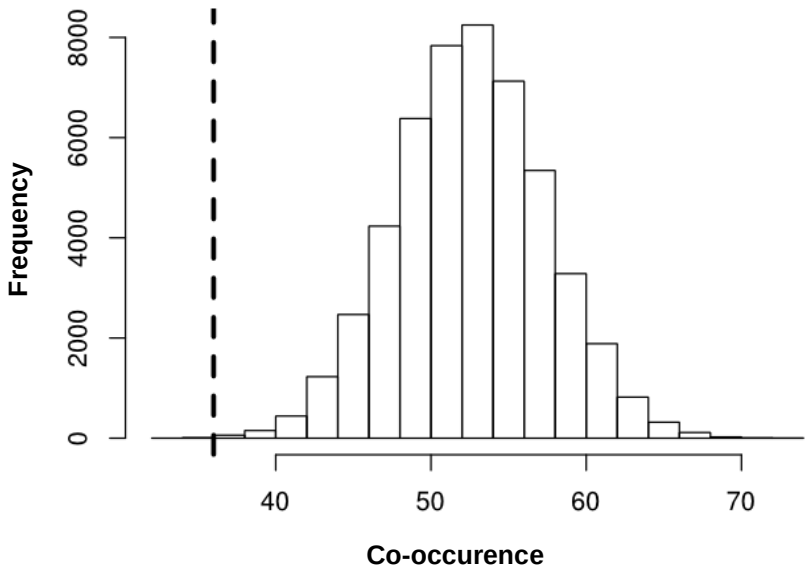
Appendices



Appendix 1. Variation in the number of *V. currens* specimens (nymphs and adults) recorded during the study period. A) sites L2-L3; B) sites M1-M3.



Appendix 2. Variation in the number of *V. gridellii* specimens (nymphs and adults) recorded during the study period. A) site L1; B) sites H1-H3.



Appendix 3. Frequency distribution of 50,000 simulated co-occurrences (SCO), according to the null-model. The vertical dashed line is the observed co-occurrence value (OCO).

Remark on polymorphism in the genus *Velia* Latreille in Italy

In *Velia* , brachyptery is restricted to a single species, *Velia* (s.str.) *rivulorum* representing a monotypic subgenus . Species of the subgenera *Plesiovelia* and *Haldwania* are only known in the macropterous and/or apterous morph. From the present character distribution of wing morphs , it is difficult to judge whether the macropterous/apterous or the macropterous/brachypterous condition is the plesiomorphic character state in *Velia* ; this requires a phylogenetic analysis of the subfamily (Tran et al., 2009).

In Italy among the species of the subgenus *Plesiovelia*, there are different ratio between macropterous/apterous morph. For example, studying museum collections and private collections (see Material and Methods), *V. muelleri* Tamanini, 1947 shows a completely different ratio from *Velia currens* (Fabricius, 1794) and *V. gridellii* Tamanini, 1947. In fact *V. muelleri*, in Central and Southern Italy, seems to be mainly macropterous, while the apterous morph is less common (ratio 1:5).

4.4 Hairy structures

Comparative description of the hairy structures in two endemic *Velia* species (Hemiptera: Heteroptera: Gerromorpha: Veliidae): *V. currens* (Fabricius, 1794) and *V. gridellii* Tamanini, 1947

Abstract. This study aims to provide a first description, based on SEM imagery, of the hairy structures related with life on the water surface, of two Alpine-Apenninic species belonging to the genus *Velia*: *V. currens* (Fabricius, 1794) and *V. gridellii* Tamanini, 1947. In general, no relevant differences in the organization and form of these structures were found between the two species. Similarly, few differences were observed between males and females, whenever comparisons were possible. Few differences were also found with the only congeneric thus far described, *V. caprai* Tamanini, 1947, confirming a substantial homogeneity within the subgenus *Plesiovelia*. The discovery of a double layer of microtrichia in both our species allowed us to detect them even in *V. caprai*, for which only a single layer was previously described. Finally, we report for the first time in the genus, and in the Old World Veliinae, the presence in females of *V. gridellii* of a structure corresponding to the grasping comb already described in males. A similar structure was not identified in *V. currens*. This difference may be relevant for better understanding the relationships among species belonging to this genus.

Introduction

Semi-aquatic bugs (Gerromorpha) are the most abundant and widespread among the insects inhabiting the upper surface of natural waters (Andersen, 1977). Their body surface is covered by a number of long and thin cuticular expansions or protrusions, generally called "hairs". Although at first sight these structures may appear quite similar, their origin, shape and function may differ considerably (Perez-Goodwyn, 2009). The analysis of hairy structures in these bugs may be interesting from two different points of view. First, since many of these structures are adaptations to life on the water's surface (e.g. Andersen, 1982), obtaining more information on their shape and distribution may help in understanding much of the biology of these organisms. Secondly, as for any other morphological trait, a comparative analysis of these structures may help elucidate the relationship among different species or groups of species.

According to Andersen (1976; 1977) two different types of hairs can be distinguished in Gerromorpha: "*macro-hairs*" and "*micro-hairs*" (also known as macrotrichia and microtrichia, respectively). Macro-hairs are flexible and inserted in sockets, while micro-hairs are stiff and appear as cuticular outgrowths. Richards and Richards (1979) pointed out that this difference in structure reflected a different origin. Macro-hairs (which they called "setae") are outgrowths originated from two differentiated epidermal cells: a trichogen cell secreting the cuticle of the protusion and a tormogen cell secreting the socket of the protusion. On the contrary, micro-hairs are subcellular processes and a single epidermal cell may show more than one projection. Micro-hair layers are a characteristic feature of semiquatic bugs, and vary greatly among species but also among body regions of the same specimen. For example, antennae, rostrum and leg segments usually present only macro-hairs, whereas other body parts may possess both types. Macro- and micro-hairs and structures derived from them may be involved in a plethora of different functions. One of the best known is to serve as anti-wetting structures and, depending on their orientation, combination and form, different degrees of water resistance may be allowed, ranging from simple waterproofing to extreme resistance to prolonged submersion (see Perez-Goodwyn, 2009).

Other known important structures are the so-called "*peg-plates*" and "*thornlike outgrowths*" (also named "sieve-pores" and "grooved setae", respectively; see Cobben, 1978). Although their origin is fairly clear, being derived from modified micro-hairs, their function is still unknown (Andersen, 1977). Peg-plates have been recorded in all gerromorphan families except Hermatobatidae and Gerridae and are ovate or circular structures, consisting of a rim enclosing a variable number of minute pegs, and distributed on the surface of the head, thorax, abdomen and – in some species – on basal segments of the legs. Thornlike outgrowths (Andersen, 1977) are, on the contrary, restricted to the Veliidae family. These peculiar structures have a deeply grooved surface,

suggesting an origin by a fusion of a group of long microtrichia, and are generally straight or slightly curved, with a thick basal part and strongly tapering apex (Andersen, 1982; Schuh and Slater, 1995). Their possible involvement in anti-wetting functionality remains an open question.

Another family of hairy structures described in all gerromorphan families are the so-called "*grooming structures*", located on the distal part of some or all tibiae. These structures are composed of modified macrotrichia, usually arranged to form combs and brushes (Andersen, 1976, 1982). Andersen (1976) reported them as having the function of "cleaning devices" used "to keep the hair layers of the legs and body tidily arranged and free of dust and water drops" (see also Rensing (1962) for a description of the grooming behaviour of various species of gerromorphan bugs).

A final type of structure is represented by "*grasping combs*" present (mainly) in the front tibia of males of the family Veliidae, first described in *Halovelia* and *Microvelia* by Hale (1926). In some species, a short grasping comb is also found in the middle tibia of males (Lundblad, 1933), while in other taxa the comb in the front tibia is greatly reduced or absent (Andersen, 1982). These structures are typically composed of numerous, densely arranged, short and stout hairs and have been hypothesized to serve a role during copulation to allow males a firm grip on the female's thorax. However, this interpretation has been questioned (Andersen, 1982) since a similar, although usually shorter, structure was described in the fore tibia of the female of some species of Veliinae (e.g. in genera *Angilia* and *Stridulivelia*, and in some species of *Paravelia*).

In the genus *Velia*, a detailed description of body hair layers and derived structures, based on scanning electron photomicrographs, is only available for the central/northern European species *Velia caprai* Tamanini, 1947 (Andersen, 1977, 1982). Little is known for more southerly species (cf. Tamanini, 1947), such as *V. currens* (Fabricius, 1794) and *V. gridellii* Tamanini, 1947. These two species are Alpine-Apenninic elements (Vigna Taglianti et al., 1999) and can be considered Italian endemics *sensu lato* (Cianferoni and Santini, 2012). The aim of this study is to fill this gap, examining the hairy structures of these two species.

Materials and methods

Adult specimens of both sexes (apterous morph), previously identified as *Velia* (*Plesiovelia*) *currens* (Fabricius, 1794) and *V.* (*P.*) *gridellii* Tamanini, 1947, were collected during spring–summer 2011 from different sites near Florence, Italy (see Cianferoni and Santini (2012) for more details). Specimens, dry mounted or preserved in 70% alcohol, were cleaned with pure ethanol and dissected under a stereomicroscope. Selected pieces were mounted on aluminium supports (stubs) covered by conductive glue, sputter-coated with graphite and gold. Prepared samples were observed using a Zeiss Evo MA15

scanning electron microscope at the Interdepartmental Center on Electron Microscopy and Microanalysis (M.E.M.A.) of the University of Florence.

For comparison of the ventral hair layers within the two species and two sexes, the same abdominal sternite (IV) and the mesosternum were chosen. Measures of macro- (n=30) and micro-hairs (n=20) were taken in the medio-basal portion of the fourth abdominal sternum and mesosternum. Widths of macro-hairs were taken in the lower third according to Andersen (1977). Peg-plates and thornlike outgrowths were measured respectively in the fourth abdominal sternite and in the mesosternum (see above).

Densities were measured in different random spots of the compared area and averaged. All measurements were taken from SEM photographs using the software package ImageJ ver. 1.46r (Schneider et al., 2012).

Results

Macro-hairs and derived structures

Macro-hair layers

Macro-hairs cover much of the body surface of both the studied species. In the ventral part of their abdomen, the macro-hair layer is uniform and composed of a single type of hairs. The typical macro-hairs are wider in the lower third, with a tapering and pointed apex (Fig. 1A) and inserted in a low socket (Fig. 1B). The surface of the hairs is fluted by longitudinal ridges and grooves (width of grooves is about 0.4 μm in both species and sexes). The size of these hairs is similar throughout the different species and sexes. In *V. currens* their length is in the range 45–90 μm, while the width (in the lower third) varies from 2.0 to 3.6 μm and the density is approximately 1,900 hairs/mm^2. Comparable values were found in *V. gridellii*, but slightly shorter and less dense hairs were found in females than males (length: 45–70 vs 55–90 μm; width: 2.5–3.3 vs 2.2–3.5 μm; density: 1,500 vs 1,900 hairs/mm^2). Macro-hairs in the sternum of both species are more variable. In *V. currens* macrotrichia range from a length of about 20 μm in the middle to about 150 μm at the sides. In *V. gridellii* these are generally longer and vary from about 30 μm long in the middle sternum to about 230 μm at the sides.

Abundant macro-hairs were also visible on the distal part of the tibia in both species (Fig. 2). These, located both in the internal and external part of the tibia, are typical bristling or long spiniform macro-hairs, recumbent and parallel to the surface. Sizes were similar in both species with lengths in the range 30–115 and 30–155 μm in *V. currens* and *V. gridellii* respectively, and widths in the range 1.5–3.3 and 1.2–4.3 μm respectively.

Macro-hairs in tarsi have slightly different forms, depending on their position (Fig. 1C). In general those in the front part of the tarsus are straight or slightly curved at the apex (Fig. 1D), and are generally larger in *V. gridellii* than in *V. currens* (length: 34–103 vs 47–78 μm; width: 1.7–4.1 vs 1.6–2.5 μm). More bristling macro-hairs with a distinctly hooked apex are more common in the lower part of the tarsus, although they are also sporadically present in its

upper part. They are about 26–56 μm long and about 1.0–1.8 μm wide in *V. currens* and 30–60 μm long and about 1.2–2.5 μm wide in *V. gridellii*. Density of macro-hairs in the tarsus (measured in the external-lateral side) is about 5,600–6,000/mm^2 in the females of both species and slightly higher in males (6,400–6,800 and 6,800–7,200/mm^2 in *V. currens* and *V. gridellii*, respectively).

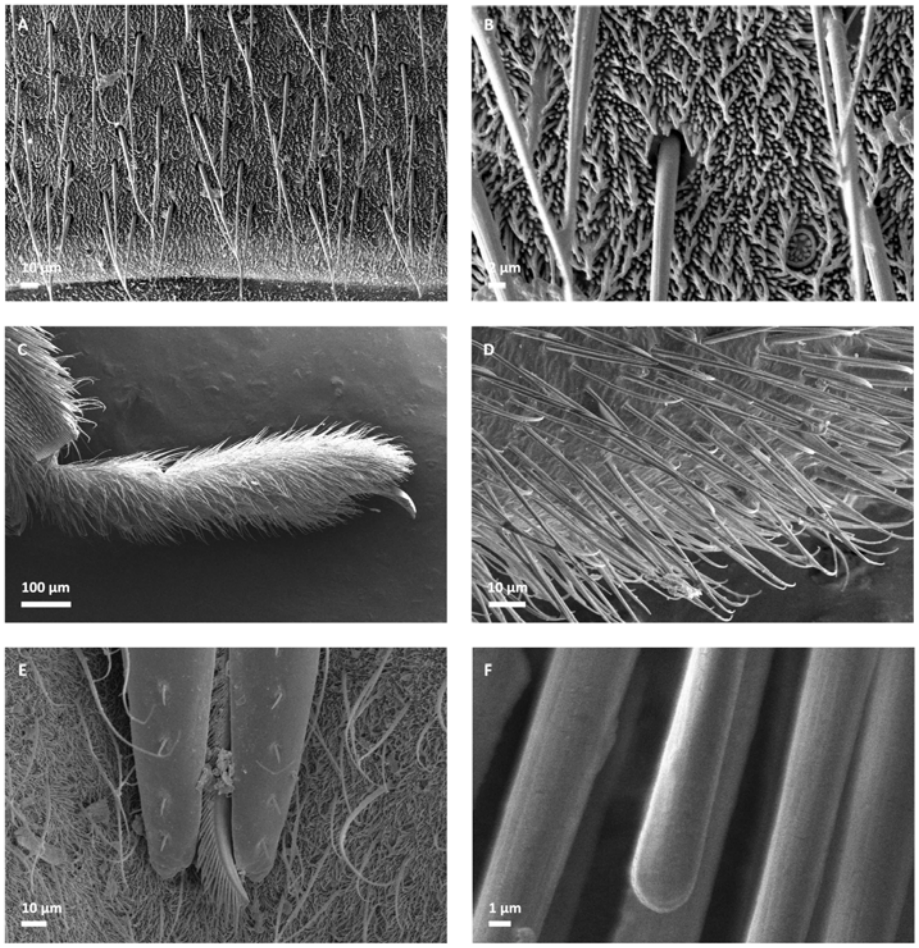


Fig. 1. Examples of macro-hairs. — A. Macro-hairs in the hind portion of the fourth abdominal sternite. *V. gridellii*, female. — B. Detail of the socket of a macro-hair (micro-hairs also visible). IV abdominal sternite. *V. gridellii*, female. — C. Overview of the macro-hairs on the front tarsus. *V. gridellii*, male. — D. Macro-hairs on the ventral side of the front tarsus. *V. currens*, male. — E. Macro-hairs disposition on the tip of rostrum. *V. currens*, male. — F. Modified macro-hairs of the hind grooming brush up the wide-tooth comb. Front tibia of *V. gridellii*, male.

Finally, macro-hairs on the coxae have highly variable lengths depending on their position. Length may range from about 8 μm long in the

basal part to about 120/165 μm (*V. currens/V. gridellii*) in the distal portion of the coxae. The rostrum of both species is mainly glabrous (Fig. 1E), with 6–8-μm-long macrotrichia in the apical part (about nine hairs for each side) and a sporadic couple of longer macro-hairs in the upper part.

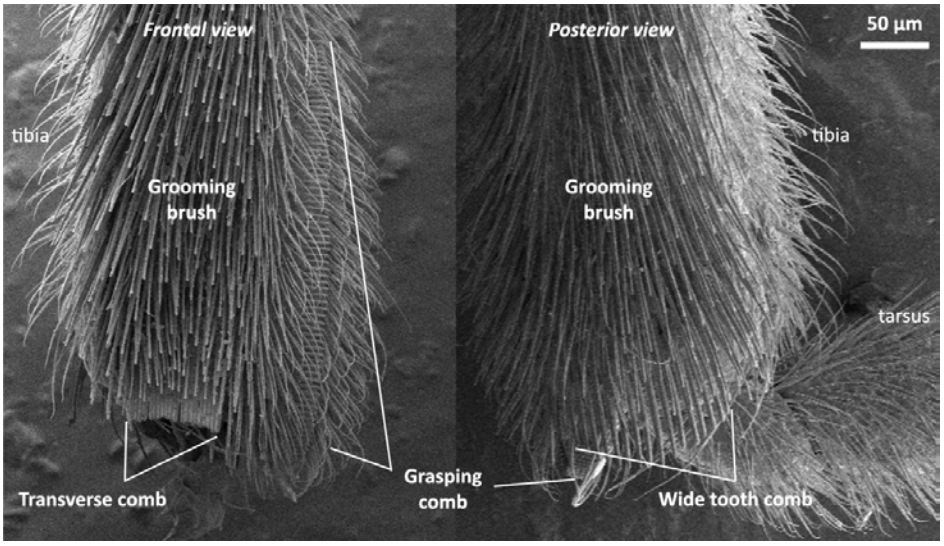


Fig. 2. Disposition of the grooming structures in the front tarsus. Frontal view (tarsus removed) and posterior view of the front right leg of *V. currens*, male.

Grooming structures

The arrangement of structures on a generalized front leg is shown in Figs 2A and 2B. Grooming structures are present in both species on the distal part of all tibiae, although they may take different forms, depending on their position. Three different types of structures can be recognised: "wide-tooth combs", "transverse combs" and "grooming brushes".

The "wide-tooth comb" (Fig. 2) is located on the posterior part (with the tarsus directed forward) of the front, middle and hind tibiae and is formed by stout spine-like hairs originated from modified macro-hairs (Fig. 4). This structure is less defined in the hind legs (see also Andersen, 1976). Wide-tooth combs are slightly smaller in *V. currens* (length: 62–72 μm; width: 3.0–3.6, 1.8–2.3 and 1.9–2.5 μm in the lower third, distal part and in the club, respectively), than in *V. gridellii* (length: 73–74 μm; width: 3.3–4, 2.1–2.4, 2.3–3.4 μm in the lower third, distal part and in the club, respectively). The apical shape of the teeth of the "wide tooth comb" is variable: sometimes tapering, and sometimes distinctly enlarged, forming a sort of club (Fig. 4).

The "transverse comb" (Fig. 2) is located in the anterior part (with the tarsus directed forward) of the tibia in the front legs, but is lacking in the middle

and hind legs. In *V. currens* the transverse comb (Fig. 3A) is about 70 μm wide. Teeth (equivalent to the "long, faintly spatulate spines" described in Andersen, 1976) are, on average, 29 μm long, 2.6 μm wide in the basal part and 3.5 μm in the enlarged apical part (Fig. 3B). In *V. gridellii*, the transverse comb (Fig. 3C) has the same structure but is slightly larger (width: 86 μm), with teeth being, on average, 35 μm long, and 3.6/4.2 μm wide in the basal/apical part (Fig. 3D).

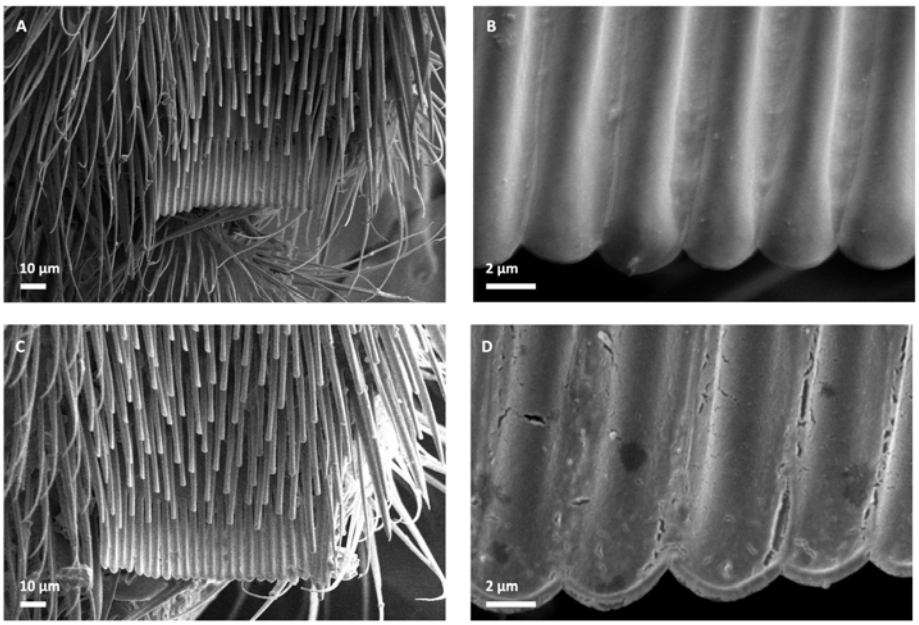


Fig. 3. Transverse combs. — A. Transverse comb of *V. currens*, female. — B. Particular of the comb teeth in the transverse comb of *V. currens*, female. — C. Transverse comb of *V. gridellii*, male. — D. Magnification of the comb teeth in the transverse comb of *V. gridellii*, female.

The "grooming brushes" are composed of club-shaped macro-hairs (equivalent to the "stout, faintly spatulate spines" described in Andersen, 1976), which are progressively shorter toward the distal part of the tibia (Fig. 1F). This structure is present in the front tibia, just on the transverse comb, and in *V. currens* is about 30–60 μm long, 2.5–3.5 μm wide in the lower third, 1.4–2.0 μm wide in the distal part, and 1.6–2.1 μm wide in the club. In *V. gridellii* the club-shaped macro-hairs of the grooming brush above the transverse comb are about 32–50 μm long, 3.0–3.5 μm wide in the lower third, 1.6–2.5 μm wide in the distal part, and 2.1–2.8 μm wide in the club. Similar grooming brushes are also present above the wide-tooth combs, but they are less defined compared to the previous, especially in the hind tibiae.

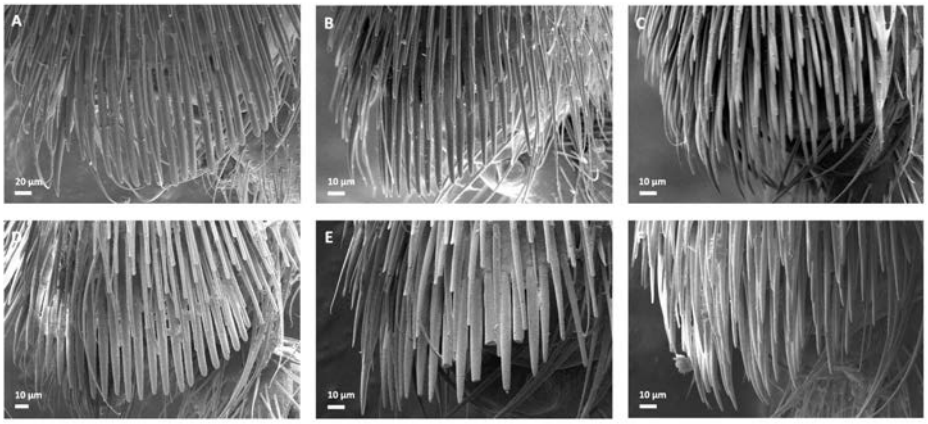


Fig. 4. Wide-tooth combs of the females of the two species. — A. Comb of the front leg of *V. currens*. — B. Comb of the middle leg of *V. currens*. — C. Comb of the hind leg of *V. currens*. — D. Comb of the front leg of *V.gridellii*. — E. Comb of the middle leg of *V. gridellii*. — F. Comb of the hind leg of *V. gridellii*.

Protibial grasping combs

These peculiar structures are composed of a stripe of short stout teeth located in the distal portion of the tibia (Fig.5A), and appear as a dark structure when seen under light microscopy (pers. obs.). The upper part of the grasping comb is parallel to the length of the tibia and clearly curves just before the tarsus. In males of *V. currens* the grasping comb is about 0.35 mm long and appears composed of slightly more than 80 teeth. Each tooth is a short straight stout spine (Figs 5B and 5C), rounded at the apex and fluted by longitudinal ridges, 0.15 µm wide. Teeth measure about 19 µm in length and are around 4.6 µm wide at the base and 3.0 µm in the apical third. In *V. gridellii* males, grasping combs are slightly longer (~0.45 mm) and composed of a number of teeth comparable to that of *V. currens*. Each tooth is a shortstout spine, distinctly curved (Figs 5D and 5E) and more rounded at the apex than in *V. currens*. The longitudinal ridges are 0.15 µm wide, as in the previous species. Measurements of the teeth are: length – around 19 µm; width at the base – around 5.8 µm; width in the apical third – around 4.2 µm. Surprisingly, grasping combs were also observed in female *V. gridellii* (Fig. 5F), where the structure is shorter than in males (less than 10 teeth, each 15–16 µm long) and located in the lower portion of the front tibiae. No corresponding structure was observed in female *V. currens*.

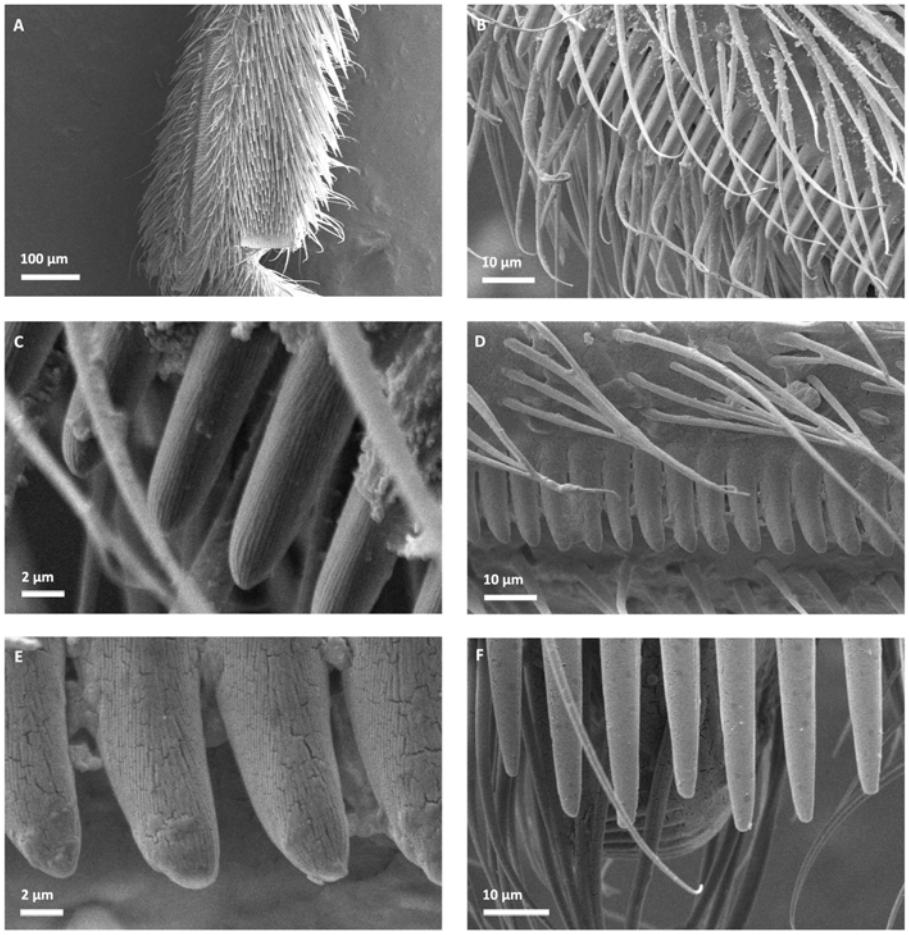


Fig. 5. Grasping combs. — A. Overview of the grasping comb of male *V. gridellii*. — B. Magnification of the teeth of the grasping comb in *V. currens*. — C. Sculpturation of teeth of the grasping comb in *V. currens*. — D. Magnification of the teeth of the grasping comb in *V. gridellii*. — E. Sculpturation of teeth of the grasping comb in *V. gridellii*. — F. Central teeth of the wide-tooth comb of female *V. gridellii*. The reduced grasping comb is visible in the background.

Micro-hair layers and derived structures

Micro-hair layers

Micro-hairs are small cuticular outgrowths present in the ventral parts of the body (Fig. 6A; also see Fig. 1B), but not on the legs, antennae and rostrum. Micro-hair dimensions vary between different body regions of the same specimen, but generally not between sexes. In the ventral part of the abdomen of *V. currens* (males and females), two distinct types of micro-hairs are recognizable. A dense basal layer of minute microtrichia about 0.7 µm long

(maximum 1 μm long) and 0.3 μm wide (range: 0.25–0.45 μm) with a density of about $12\times10^5/mm^2$. From this base layer, longer (4.5 μm; range: 3.0–5.0 μm) and less dense (about $3–3.5\times10^5/mm^2$) microtrichia sprout (around 0.45 μm wide; range: 0.35–0.55 μm), forming a second layer. The same microtrichia values were obtained from measurements of *V. gridellii*, except for the second layer with longer (3.5 μm; range: 2.5–4.5 μm) and wider (0.40 μm; range: 0.30–0.50 μm) microtrichia.

Longer micro-hairs in the sternum have a variable length (*V. currens*: 3.5–9.0 μm; *V. gridellii*: 2.5–9.5 μm) but are more constant in width (*V. currens*: 0.35–0.70 μm; *V. gridellii*: 0.40–0.60 μm) (measurement taken in the lower third). Their density, about $8\times10^5/mm^2$ in both species, is higher than in the abdomen. In both species there are also shorter and more subconical micro-hairs (length: 0.7–1.8 μm) with a higher density ($12\times10^5/mm^2$).

Peg-plates

In *V. gridellii* (Figs. 6B) these structures are slightly ovate with diameter ranging from 4.2 to 4.9 μm. The plate is bounded by a 0.45 μm wide rim, and occupied by 12–16 pegs. The pegs, slightly subconical, measure 0.6–0.7 μm in length and are 0.35–0.40 μm wide. In the abdomen the density of these structures is around $1{,}600/mm^2$. In *V. currens*, peg-plates have a shape similar to that of the other species, although their size (diameter: 3.5– 4.1 μm; rim width: 0.35 μm) is smaller, and the number of pegs per plate (10–12) less. The size of pegs and the density of plates are similar to *V. gridellii*. No evident differences were found between males and females.

Thornlike outgrowths

These structures, which are straight or slightly curved, appear to be deeply grooved, supporting the hypothesis that they originate from the fusion of several long microtrichia (Figs 6C and 6D). Their shape is rather variable, but usually presents a thick basal part and a strongly tapering apex with, in some cases, a sort of cap on the top (Fig. 6C). In a few cases, a drop-like structure form was detected on their tip (Fig. 6D). In *V. currens* the length of thornlike outgrowths falls in the range 9–13 μm, and the width in the ranges 2.6–2.9 μm and 0.5–0.7 μm at the base and apex respectively. Distances of the grooves are highly variable (0.2–0.9 μm). We estimate 14–18 microtrichia for each structure. The density in the sternum is about $3–400/mm^2$. In *V. gridellii* thornlike outgrowths are 8–11 μm long, with widths of about 3.0–3.5 μm and 0.3–0.6 μm at the base and apex respectively. Distances of the grooves are variable (0.2–0.8 μm). We estimate that the structures are composed of 10–16 microtrichia.

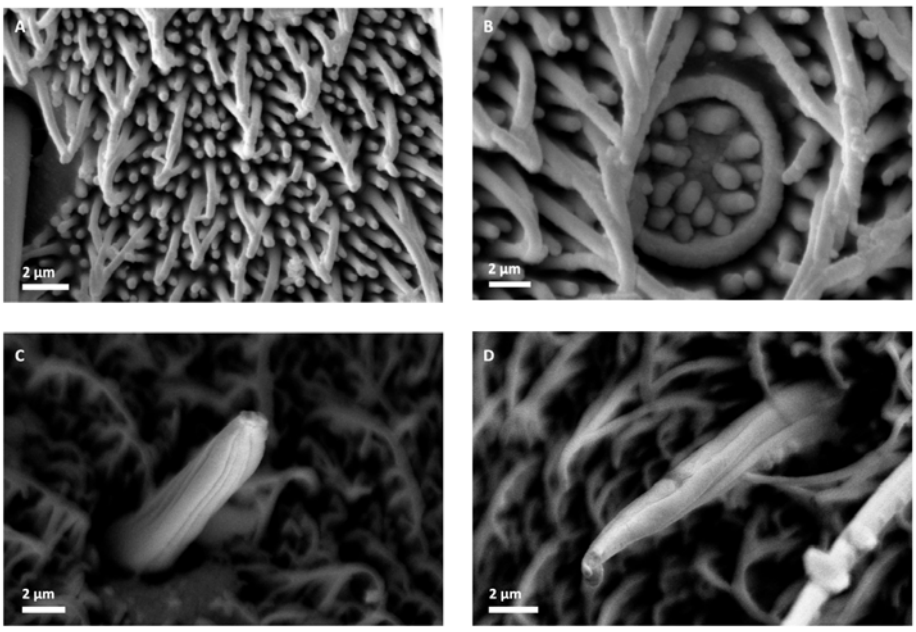


Fig. 6. A. Micro-hairs double layer at higher magnification. IV abdominal sternite. *V. gridellii*, female. — B. Peg-plate in the abdomen (IV sternite) of *V. gridellii*, female. — C. Thornlike outgrowth in the mesosternum of *V. currens*, female. — D. "Drop" on the tip of a mesosternal thornlike outgrowth in a male of *V. currens*.

Discussion

This study provides a first detailed description of some of the hairy structures in two Alpine-Apenninic endemics, *V.gridellii* and *V. currens*, based on SEM imagery. In general, no relevant differences in the organization and form of these structures were found between the two species. Similarly, little differences were observed between males and females, whenever comparisons were possible. Specifically, body macro-hairs have similar form and arrangement in the two species and sexes, although *V. gridellii* appears to be more glabrous than *V. currens*, and hairs are slightly longer and denser in males than females. According to the data presented by Andersen (1977) the congeneric *V. caprai* would seem to be less hairy than our two species (1,000 vs 1,500–1,900 macro-hairs/mm^2, respectively), although unambiguous comparisons are hardly possible because the author did not specify the body district where density measurements were taken, nor the sex of the samples. Indeed, densities were found to vary greatly in different parts of the body in our species. In the front tarsus of *V. currens* and *V. gridellii* we also identified two types of hair (a short and mainly curved type and a longer and more straight type), but we did not find a strict categorization, with specific types of hair

located in rows, as indicated by Andersen (1976) for the middle tarsus of *V. caprai*. The density of the macrotrichia is comparable for the two species, but distinctly higher in the males.

Two distinct types of micro-hair layers were also identified in the two species: a basal layer of short microtrichia and an upper layer of longer microtrichia. This finding contrasts with the results presented by Andersen (1977) for *V. caprai*, where a single layer of micro-hairs was described. However, a closer look at the images published in that paper (see Andersen, 1977; Figs 13 and 35) suggests that two distinct layers of micro-hairs did in fact exist in that species. Furthermore, although the author never explicitly mentions the existence of two distinct layers of microtrichia, he talks about "long microtrichia" to explain the origin of thornlike outgrows (see below), leading the reader to understand that different types of microtrichia may exist.

Peg-plates are similar in the two studied species, although they are slightly bigger in *V. gridellii* and, accordingly, contain a greater number of pegs. These structures are comparable, in shape and size, with those described by Andersen (1977) for *V. caprai*, but their density in our species is apparently lower than in *V. caprai*. On the contrary, the structures described in our two species (and also in *V. caprai*) appear to be clearly smaller than those observed in some members of more primitive gerromorphan groups, such as Mesoveliidae, Hebridae, Macroveliidae and Hydrometridae (cf. Andersen, 1977).

The shape and form of thornlike outgrowths, which appear to be deeply grooved in both species, support the idea that these structures may originate from the fusion of several long microtrichia, as first hypothesized by Andersen (1977). Dimensions of the thornlike outgrowths are comparable within the two studied species, but the structures seem more slender in *V. currens* than in *V. gridellii*. They also appear to have similar dimensions to those in *V. caprai*, but this is based solely on measurements taken from the single published image of a thornlike outgrowth of *V. caprai* (Andersen, 1977), which of course has its limitations. Investigation into the function of the observed structures is out of the scope of this study; however, the observation of drop-like forms at the apex of thornlike outgrowths could suggest a secretory function of these structures, although this hypothesis needs stronger evidence than this to be confirmed.

Similar to other structures, all the elements involved in grooming structures (combs, teeth, hairs etc.) are generally larger in *V. gridellii*, in accordance with this species' overall larger size. A comparison with *V. caprai* is not possible because the grooming structures have been described only generically by Andersen (1976) with no details (e.g. number of spiniform hairs, etc.) and without publishing any SEM images. It is important to note that, in the processes forming the grooming combs, sockets were clearly visible (see Figs 3C, 4E). This finding suggests that the term "spines", used in previous literature (e.g. Andersen, 1976, 1982) for these structures in *Velia* seems incorrect and should be avoided (cf. Andersen and Weir, 2001), at least if we

follow the classification proposed by Richards and Richards (1979). According to this classification, spines or thorns are multicellular processes which lack specialized cells in the underlying epidermis and are also recognizable by the absence of a socket. Some modifications are made to the definition and terminology of the grooming structures. The “wide-tooth comb” (Fig. 2) is a structure that Andersen (1976) indicates as a “grooming structure”, composed of a “system of apical spines on the hind surface of the […] tibia […] not forming a distinct grooming comb”, and that we renamed to avoid confusion with other elements involved in grooming. The “transverse comb” is a structure named by Andersen (1976), but also indicated by the same author as the only real “grooming comb”. Finally, “grooming brush” is a term that Andersen (1976) uses specifically only for *Halobates flaviventris* (Gerridae), but in our opinion can also be extended to the hairs located above the combs previously cited.

However, the main finding regarding grasping combs in the present study is the detection of these structures in the front tibiae of female *V. gridellii* as well as males. The structure is very short in females and not as well developed as in males, and its teeth are smaller. Furthermore, no similar structure was observed in *V. currens*. This finding, however, supports the idea that these structures may have (or may originally have had) other functions not related to grasping of females by males, as previously suggested by their detection in females of other Veliinae, such as in the genera *Angilia* and *Stridulivelia*, and in some species of *Paravelia* (Andersen, 1982). It is unclear if the female structure is due to secondary reduction, as hypothesized by Andersen (1982) based on their absence even in males of some species of Microveliinae, Veliinae, Ocelloveliinae. This discovery is the first for the genus *Velia*, but also for the Old World Veliinae; besides, it strengthens this synapomorphy (presence of a grasping comb in the female) and consequently the monophyly of the subfamily as well.

The presence of a female grasping comb in *V. gridelli* but not in *V. currens* supports the idea that these two species, although both being Alpine-Apenninic endemics, may probably belong to different groups of species. *V. currens*, in fact, mostly on the basis of the male parameres and endosomal sclerites and female abdominal shape, has been proposed to belong to a European group of species, while *V. gridellii* seems to be the most western species of a Turano–Mediterranean group (Cianferoni and Mazza, 2012). Finally, the lack of this comb (possibly because of secondary reduction) in *V. currens* and *V. caprai* (cf. Andersen, 1982) also seems to suggest a greater affinity between these two species than with *V. gridellii*.

Conclusion

The descriptions and SEM images provided in the present study constitute the first data on hairy structures in *Velia currens* and *V. gridellii*. The comparison between the two species and (when possible) with *V. caprai*, the

only other known species of the genus, revealed only weak differences, confirming a substantial homogeneity within the subgenus *Plesiovelia* Tamanini, 1955. The discovery of a double layer of microtrichia in both species analysed in the present study led us to detect them even in *V. caprai*, for which only a single layer was previously considered by Andersen (1977). Finally, we reported for the first time in the genus *Velia*, and in the Old World Veliinae, the presence in *V. gridellii* females of a structure corresponding to the grasping combs already described in males. A similar structure was not, however, identified in *V. currens*. This difference may be relevant for understanding better the relationships among species belonging to this genus. Further studies are nevertheless needed to verify this finding for other *Velia* species.

Acknowledgements

Our sincerest thanks go to Luca Bartolozzi (MZUF - Natural History Museum of the University of Florence, Zoological Section) for allowing access to museum facilities; Maurizio Ulivi (M.E.M.A., University of Florence) for the SEM sessions; Simone Cianfanelli (MZUF), Michele Zilioli (Natural History Museum of Milan), Simone Marini and Mario Boni Bartalucci (MZUF) for their precious advice and assistance during the preparation of the samples; and Fabio Terzani (MZUF) for helpful comments on the manuscript.

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4.5 Grooming behaviour

On the grooming behaviour of two Alpine-Apenninic species of *Velia* Latreille (Hemiptera, Heteroptera, Gerromorpha, Veliidae)

Abstract. The grooming behaviour is described and compared in two species of the genus *Velia*: *Velia* (*Plesiovelia*) *currens* (Fabricius, 1794) and *V.* (*P.*) *gridellii* Tamanini, 1947.
This behaviour is extremely similar in the studied two species, and only few differences were noted. At the same time the grooming behaviour may be highly variable even within the same species, with some steps sometimes being skipped.

Introduction

In Gerromorpha, the term "grooming behaviour" indicates a series of regular tidying and cleaning actions, performed to arrange the waterproofing hair layers throughout the body surfaces and maintain them free from debris (cf. Andersen 1982).

The first and only description of this behaviour available for the Gerromorpha is that by Rensing (1962), who described a regular series of cleaning actions, which he named "Putzbewengungen" (= "cleaning movements") or "Baden" (= "bath"), in three different species belonging to three different families (*Hydrometra stagnorum* L., 1758, *Velia caprai* Tamanini, 1947 and *Gerris lacustris* L., 1758). This behaviour was later also quoted by Andersen (1976; 1982) simply as "grooming". Unfortunately, Rensing (1962) provided a generalized description of this behaviour, merging observations taken on different species. *Hydrometra stagnorum* shows slower movements and a preferentially specular grooming, while *Velia caprai* and *Gerris lacustris* show often unilateral grooming with faster actions. Available data, therefore, does not allow to identify differences between different genera or species.

Concerning its function, Rensing (1962) showed, thorough simple experimental tests, that this behaviour is stimulated when the animals swim on dirty water or when in contact with chemical substances and inferred thus its "cleaning" function. A similar conclusion was reached by Andersen (1976; 1982), who also stressed that this behaviour not only serves to remove any impurity and water from the hairs but also to keep the hair layers tidily arranged to prevent the entry of water between them.

The aim of this note is to describe and compare this behaviour in two poorly known south European species (Cianferoni and Santini, 2012) belonging to the genus *Velia* Latreille: *V. currens* Fabricius, 1794 and *V. gridellii*

Tamanini, 1947. An accurate description of the structures involved in the grooming behaviour of these two species is available in (Cianferoni and Santini, *under review*).

Material and methods

Living nymphs and adults of both sexes, previously identified as *Velia* (*Plesiovelia*) *currens* (Fabricius, 1794) and *V.* (*P.*) *gridellii* Tamanini, 1947, were collected for this study. We used only specimens belonging to the apterous morph because of the rarity of the macropterous one (see Cianferoni and Santini, 2012). All the specimens were sampled in different localities around Florence (Central Italy), from sites where the ecology of this two species has been previously investigated (Cianferoni and Santini, 2012).

Individuals were singly inserted in a plastic dish (diameter 22.5 mm) half-filled with water and their behaviour observed and filmed under a stereo microscope. Ten adult specimens were observed for each species (5 males and 5 females) and each individual was filmed for 5 minutes each. Additionally, two nymphs were observed for each larval instar of each species. Following the same protocol. Observation on mutilated specimens were occasionally conducted on specimens that lost legs during sampling or transport.

Several structures are involved in this behaviour. These are complex structures, composed by modified macrotrichia, usually arranged in combs and brushes, and placed on the distal part of the tibiae. Although a complete description of these structures is beyond the aim of this paper (see Cianferoni and Santini, submitted, for further details) the following structures are worth mentioning: a) "*wide tooth combs*": the grooming combs located in the internal apical portion of all the tibiae, opposite to the tarsi; b) "*transverse comb*": the grooming combs located in the external apical portion of the front tibiae, between tibia and tarsus; c) "*grooming brushes*": a series of modified hairs present both on the previous structures.

Results

Grooming behaviour appears to follow a sequence of different steps, each corresponding to a different body part (Fig. 1). These are: i) front tarsal rubbing (Fig. 1a), ii) antennal grooming (Fig. 1b); iii) legs (front, middle, hind) grooming (Fig. 1c-e); iv) abdomen grooming (Fig. 1f). Apart from step i), which seems to be related to the cleaning of grooming devices (see below) and it is usually performed at start, the sequence is not regular. After rubbing, grooming usually starts from either the antennae or legs. In *V. gridellii*, the sequence started from antennae in 5 out of 10 cases, the other five being: 4 from middle legs and 1 from posterior legs. On the contrary, in *V. currens* grooming started preferentially from legs (8 cases: 5 middle, 3 posterior) and only in two cases from antennae. In general, after start, a progression of the sequence from anterior to posterior parts seems to take place.

In general, tarsal rubbing antennal and middle legs grooming are performed more often than other activities, which may also be skipped. It can occur also a simultaneous grooming on both side: mirror-like e.g. contemporary hind legs grooming (Fig. 2a) or asymmetrical e.g. a middle leg grooming on the left side and a hind leg grooming on the right side (Fig 2b).

Another behaviour observed several times in both species, during the grooming sequence, is the "reversal" (Fig. 2c). The specimen flexes one of the hind legs, plants the front legs on the water surface, then pushes itself leveraging with their middle legs. Always use the back of the abdomen as a pivot. Here follows a detailed description of the different steps.

Front tarsal rubbing

The front tarsi are rubbed together (Fig. 1a). Only the macrohairs at base of tarsi and the "wide tooth combs" seem to take place in this mechanism. This behaviour occurs before and after the cleaning of antennae and legs. In both species, the tip of the rostrum is recurrently approached to the rubbing front tarsi, but without a distinct grooming on the rostrum.

Antennal grooming

This behaviour takes place with both the front legs cleaning together the antennae (Fig. 1b). Cleaning starts from the second antennal article and proceed towards the distal one. The first antennal segment is not interested by this activity. The passage of the tarsi on each antenna is usually repeated more than once: 1 to 4 times (usually 2-3) in *V. currens* and 2 to 6 times (usually 4-5) in *Velia gridellii* and this difference was statistically significant (Mann-Whitney $W = 0.5$, $P = 0.0036$). The grooming of antennae is usually preceded by a variable number of "tries" (cf. Rensing 1962): tarsi are positioned around the antenna apparently to find the correct position, after a variable number of tries the proper grooming action started). The number of tries, usually 3-4 per antenna did not differed between species ($W = 29$, $P= 0.2806$). Sometimes after a first try this behaviour can be interrupted and does not restart. In *V. currens*, grooming always started from the right antenna, while in *V. gridellii* started indifferently from both. The antennal grooming can also be done on both coupled antennae at the same time.

Legs grooming

Front legs auto-grooming

The front legs clean themselves (Fig. 1c). Firstly tarsus against tarsus (see front tarsal rubbing), then working from the femur to the tibia. All the grooming structures seem to be involved in this activity.

Middle legs grooming

The front legs clean the tibia and tarsus of the middle legs (Fig. 1d), but the middle femur is not affected by the grooming. The use of the “wide-tooth comb” and the “transverse comb” alternates. Even the “grooming brushes” take part to the activity, flowing clearly on the tibia and the tarsus. The movements alternate from the base to distal portion of the middle leg and back, occurring several times without a fixed pattern. Also the middle legs move backwards and forwards, following the front legs movement. During this cleaning operation, the opposite front leg (not involved in the grooming) is held in a central position, in front of the head as support for balance. This behaviour could be perfectly symmetrical, occurring independently on either the right or left side.

Hind legs grooming

The middle legs clean the hind legs (tibia and tarsus), according to the same pattern and the same manner of the previous mechanism. Middle legs and hind legs both move backwards and forwards (Fig. 1d).

Abdomen grooming

The hind legs clean the lateral portions of the abdomen and the genital structures (Fig. 1e). All the grooming structures from the “wide tooth comb” to all the “grooming brush” were used. The hind leg cleans both the ventral lateral side of the abdomen and the dorsal one.

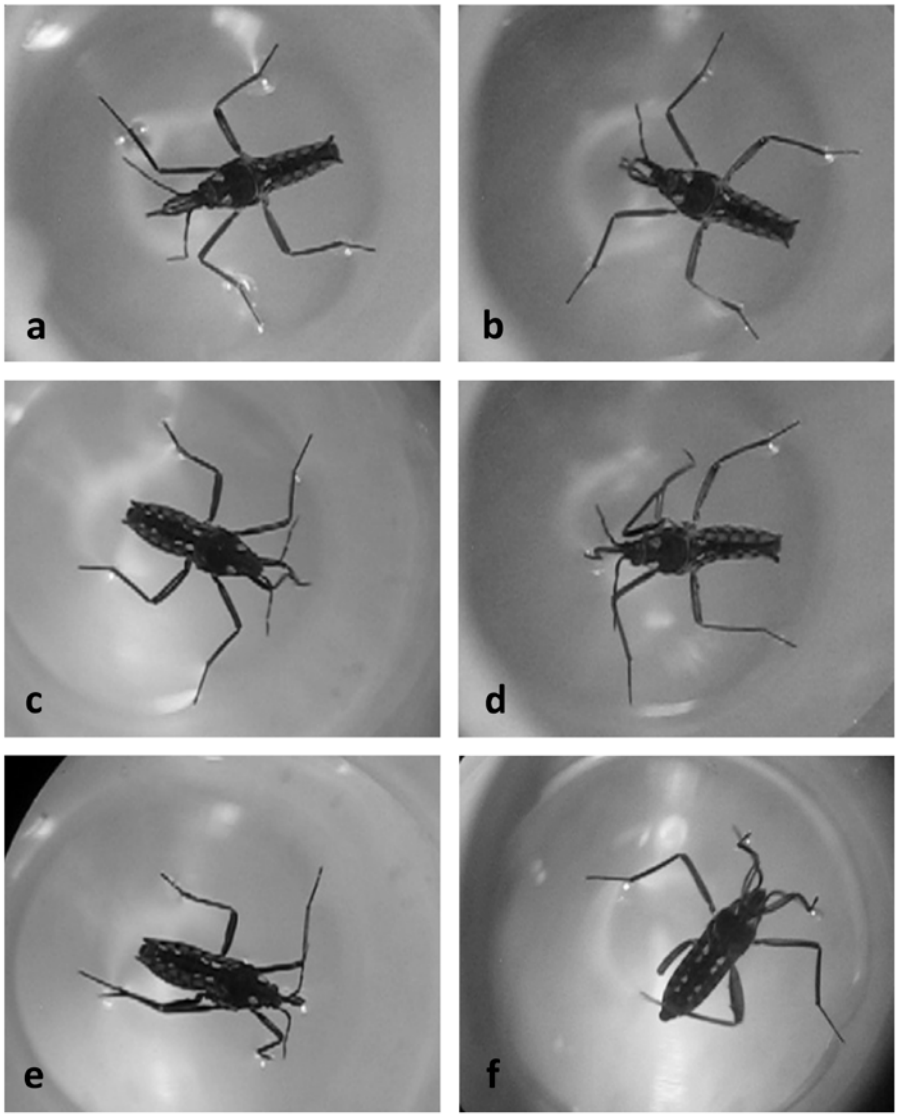

Fig. 1. Examples of the grooming behaviour. a) Front tarsal rubbing, *Velia gridellii* female. b) Antennal grooming, *V. gridellii* female. c) Front legs auto-grooming, *V. currens*, female. d) Middle legs grooming, *V. gridellii* female. e) Hind legs grooming, *V. currens*, female. f) Abdomen grooming, *V. gridellii*, male.

Discussion

Results of this preliminary study showed that grooming behaviour may be highly variable even within the same species, with some steps sometimes being skipped. What drives and triggers each step is still unknown and deserves further investigations. Interestingly, occasional observations carried out on mutilated specimens, showed the occurrence of cleaning movement also on missing legs (Fig. 2d). This may suggest that once the "pattern" has started, this action is not modulated by way of feedback from the area that has been cleaned.

The behaviour is extremely similar in the two species, and only a few differences were noted such as a different number of passages over the antennae (less in *Velia currens* and more in *V. gridellii*) during their grooming. Nymphs seem to have the same grooming behaviour of adults.

Fig. 2. a) Mirror-like grooming on hind legs, *Velia currens*, female. b) Contemporary grooming on left middle leg and on right hind leg, *V. currens*, female. c) Reversal behaviour, *V. currens*, female. d) Grooming on mutilated hind leg, *V. gridellii*, male.

Considering that these two species are phylogenetically distant, this behaviour is probably a plesiomorphic carachter, such as has been noted in the subgenus *Plesiovelia* Tamanini, 1955. In fact the two species are both Alpine-Apenninic endemics, but they belong to two different groups. *Velia currens* belong to an European group of species, while *V. gridellii* seems to be the most Western species belonging to a Turano-Mediterranean group (cf. Cianferoni and Mazza, 2012).

The observation of the approaching of the rostrum to the rubbing tarsi of both species is consistent with Andersen's observation (1976) of *V. caprai* that the maxillary stylets in the rostrum often "licks" the apices of the front tibiae, a behaviour supposed to be related to the removal of debris and water drops from the "grooming structures". However, a different hypothesis, i.e. that the rostrum may produce some hydrophobic secretion that then can be spread on all hair layers by the grooming structures, cannot be ruled out. The role of hydrophobic substances as a water-proofing mechanism has been repeatedly proposed by several authors, although this remains highly speculative (Andersen, 1982). Brinkhurst (1960) suggested the role of a hydrophobic secretion from the metasternal gland in the waterproof function for *Aquarius najas* (Gerridae). Staddon (1972) experimentally proved this hypothesis to be incorrect, at least for on *A. najas*, trough sealing the external opening of the gland and which caused no detectable effect on the ability of body hair-pile to resist wetting. Linsenmair and Jander (1963) observed that the movements of *V. caprai* are initiated by the spread of a detergent fluid (probably saliva ejected by the salivary pump through the rostrum) which lowers the surface tension of water (Andersen, 1982). In synthesis, the possibility of other types of secretions enhancing hydrophobicity or increasing wettability in Gerromorpha, as in certain beetles (Dettner, 1985), remains open (Perez-Goodwyn, 2009).

If a substance exist however is improbable that could secreted externally by a gland and then taken by rostrum because the distance from rostrum and the metathoracic scent orifice seems too large for ensures that the rostrum could withdraw the substance externally from the scent gland (Fig. 3).

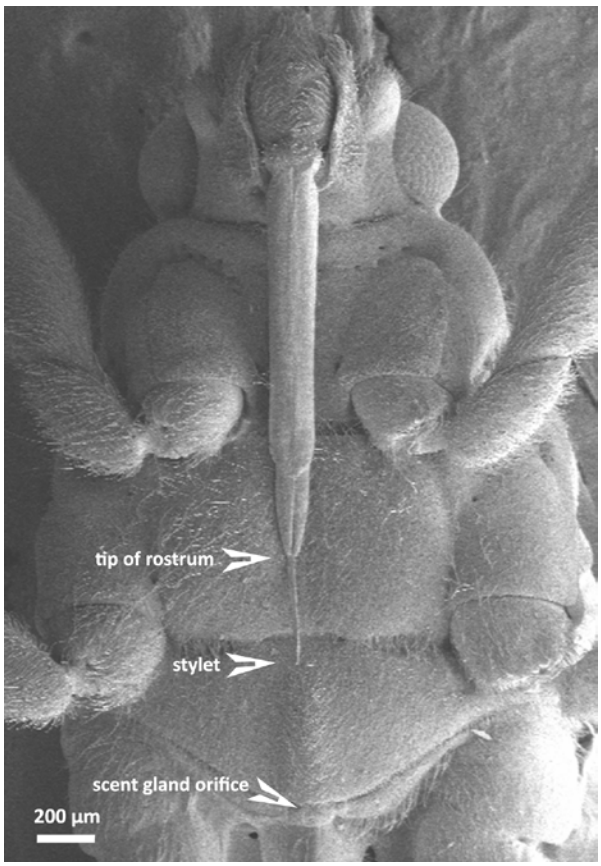

Fig. 3. Rostrum and scent gland orifice. *Velia gridellii*, male.

Acknoledgements

We wish to thank Tullio Terzani (Zeltweg, Austria) e Fabio Terzani (MZUF) for the translation of the paper of Rensing (1962).

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4.6 Contact behaviour

Preliminary observations on the "contact behavior" of the semi-aquatic bug *Velia gridellii* Tamanini, 1947 (Hemiptera: Heteroptera: Veliidae)

Abstract. This behaviour, observed under natural and laboratory conditions in *Velia* spp., consists in interactions ("collisions") among the specimens and is for the first time named "contact behaviour". Preliminary observations on *Velia gridellii* Tamanini, 1947, through the analysis of the networks representing the contacts between specimens of this aquatic insect, did not allowed to evidence any difference between males and females, neither in their degree of connection with other specimens, nor in the role they played.

Introduction

Velia gridellii Tamanini, 1947 is an Alpine-Apenninic semi-aquatic bug (Heteroptera: Gerromorpha) inhabiting calm-water areas of streams (cf. Cianferoni & Santini, 2012). This species, as other *Velia* spp. is a gregarious insect (cf. Andersen, 1982), usually occurring in "schools" of tens of individuals. It is a common observation that these aquatic insect interact with each other by "collisions". Specimens perform straight and fast movements until they collide with a nearby conspecific. Although this behaviour is very common and it is easily observed either under natural and laboratory conditions, it has never been mentioned (cf. Andersen, 1982) and its meaning is still unknown. In this note I applied standard network analysis techniques to investigate if any difference in this behaviour exists between males and females.

Materials and method

Adult specimens of both sexes (apterous morph), previously identified as *Velia* (*Plesiovelia*) *gridellii* Tamanini, 1947, were collected in mid-May 2011 in a stream pond in the Province of Florence, Tuscany, Italy (Fosso di Cercina Vecchia, Canneto, Cercina). Twentyfour specimens (12 males and 12 females) were selected and marked using nail varnish (cf. Vojířová and Ditrich, 2009) with a three-colors combination (white, blue and pink; Tab. 1). One spot was painted on the pronotum, and two on the anterior and posterior abdomen. Marking was perfomed freezing the specimens for 5 minutes to reduce their activity.

Marked specimens were then put in a light-colored plastic basin (internal diameter of 36 cm) half-filled with water. After a short period of acclimatization, they were filmed in HD with a photo camera Canon EOS-5D.

Video files of different length were selected, skipping first 30 seconds of each one to avoid interference by operators. Three videos of 6:20 minutes

(Video 1) and of about 11:00 minutes (Video 2 and 3) were chosen to build the networks.

The following variables were recorded on a spreadsheet at each contact: time of contact, code of the specimen colliding to another (hereafter defined as "actor"), code of the specimen being impacted ("receiver").

To visualize and analyze the interactions among specimens, standard social network analysis tools were used (Croft et al., 2008). For each node (i.e. each individual) in a network the following centrality measures were taken: i) degree, ii) betweenness and iii) closeness. The degree of a node is simply computed as the number of edges (i.e. connections with other nodes) connected to it. The betweennes of a given node *i* is defined as the total number of shortest paths between pairs of nodes (other than i) that pass through i. Finally closeness is an inverse measure of centrality and it is the extent to which a node is close from all other nodes.

The softwares Ucinet 6 (v. 6.421) (Borgatti et al. 2003) and NetDraw (v. 2.123) (Borgatti, 2002) were used respectively to analyze and visualize the networks. The subsequent analyses were carried out using the R (ver. 2.13.1) software package (R Development Core Team, 2011).

No.	**Code**			**Sex**
01	**B**	**B**	**B**	♀
02	**P**	**P**	**P**	♀
03	**W**	**W**	**W**	♀
04	**B**	**B**	**P**	♂
05	**P**	**B**	**B**	♂
06	**W**	**W**	**P**	♂
07	**W**	**P**	**W**	♀
08	**W**	**P**	**P**	♀
09	**P**	**P**	**W**	♀
10	**B**	**P**	**B**	♂
11	**B**	**P**	**P**	♂
12	**P**	**B**	**P**	♂
13	**W**	**W**	**B**	♀
14	**W**	**B**	**W**	♀
15	**W**	**B**	**B**	♂
16	**P**	**W**	**W**	♀
17	**P**	**W**	**P**	♂
18	**B**	**W**	**W**	♀
19	**B**	**W**	**B**	♂
20	**P**	**P**	**B**	♂
21	**P**	**W**	**B**	♂
22	**B**	**W**	**P**	♀
23	**B**	**P**	**W**	♀
24	**W**	**P**	**B**	♂

Tab. 1. Coding of the specimens. B=blue, P=pink, W=white. First two letters from left are the marking on the posterior ans anterior abdomen, third letter is the spot on the pornotum.

Results

The networks obtained from the analysis of data, for each recording (Video 1 to 3) are shown in Figs 1-3. Visual inspection of the networks does not revealed any clear pattern, related to sex, since no clear segregation between males and females was observed (e.g. individuals of one sex occupying the central part of the network). This pattern was confirmed by the analysis if centrality measures, since none of the above measures was significantly different between males and females (Table 2).

Recording	**Measure**	**Wilcoxon test (W)**	***P***
1	Degree	44.5	0.1082
1	Betweenness	41.5	0.08085
1	Closeness	99.5	0.1082
2	Degree	65	0.6991
2	Betweenness	79	0.7125
2	Closeness	79	0.6991
3	Degree	72.5	1
3	Betweenness	86.5	0.4147
3	Closeness	71.5	1

Table 2. Centrality measures.

Finally males and females were equally involved as “actors” and “receivers” (Table 3).

Recording	**Role**	**Wilcoxon test (W)**	***P***
1	Actor	44.5	0.119
1	Receiver	90	0.3115
2	Actor	61	0.5437
2	Receiver	93.5	0.2212
3	Actor	70.5	0.9539
3	Receiver	60.5	0.5253

Table 3. Comparison of the number of times males and females were engaged as actors and receivers.

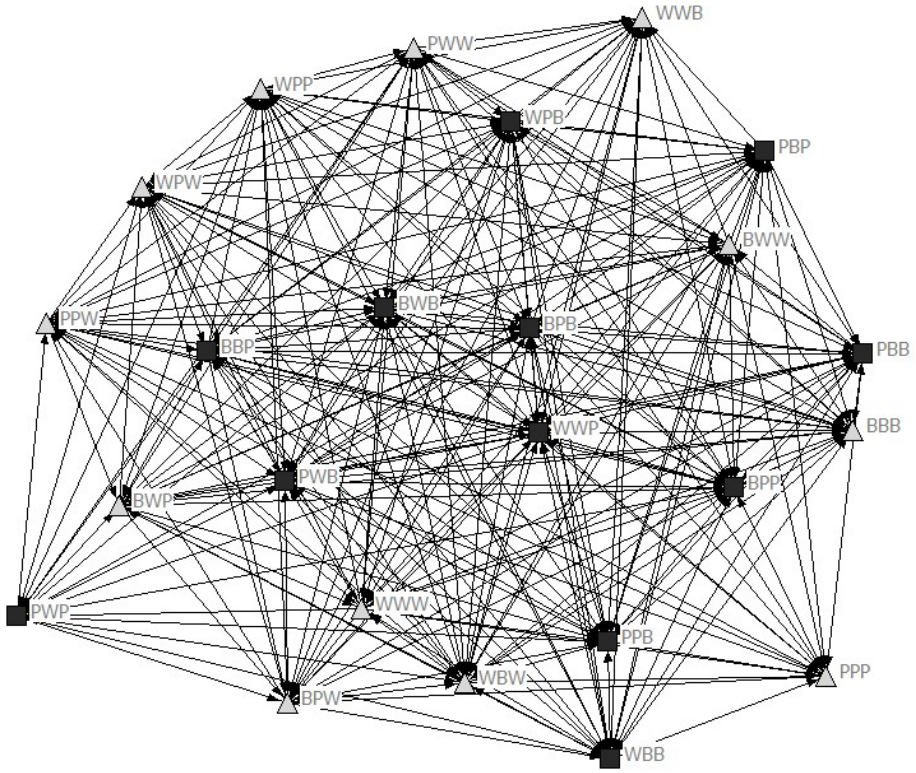

Fig. 1. Video 1 network visualization. Males are represented by dark square, females by light triangles.

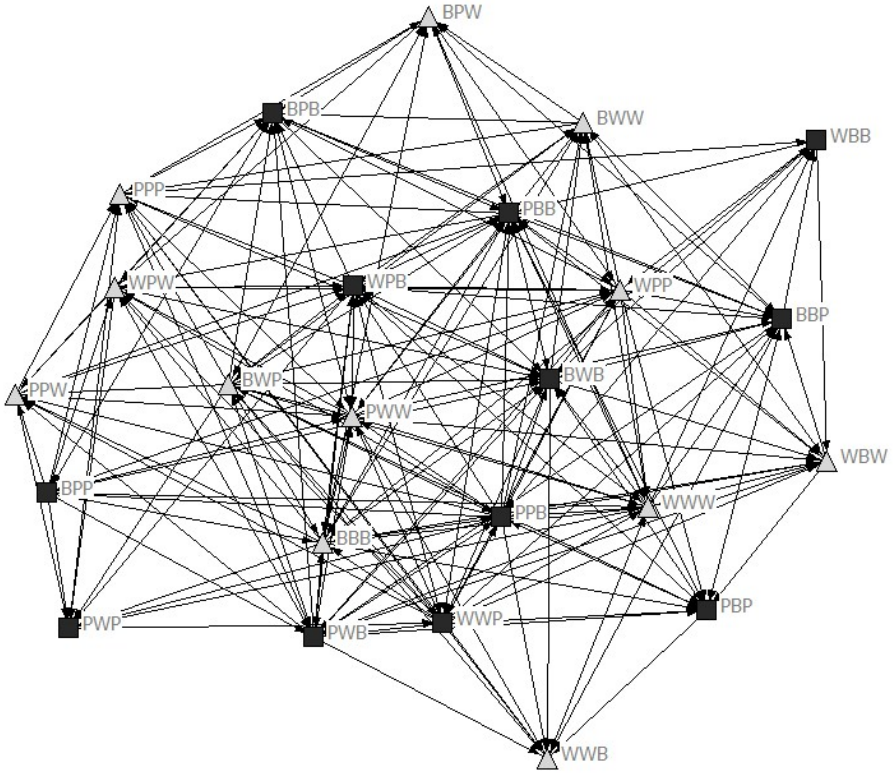

Fig. 2. Video 2 network visualization. Males are represented by dark square, females by light triangles.

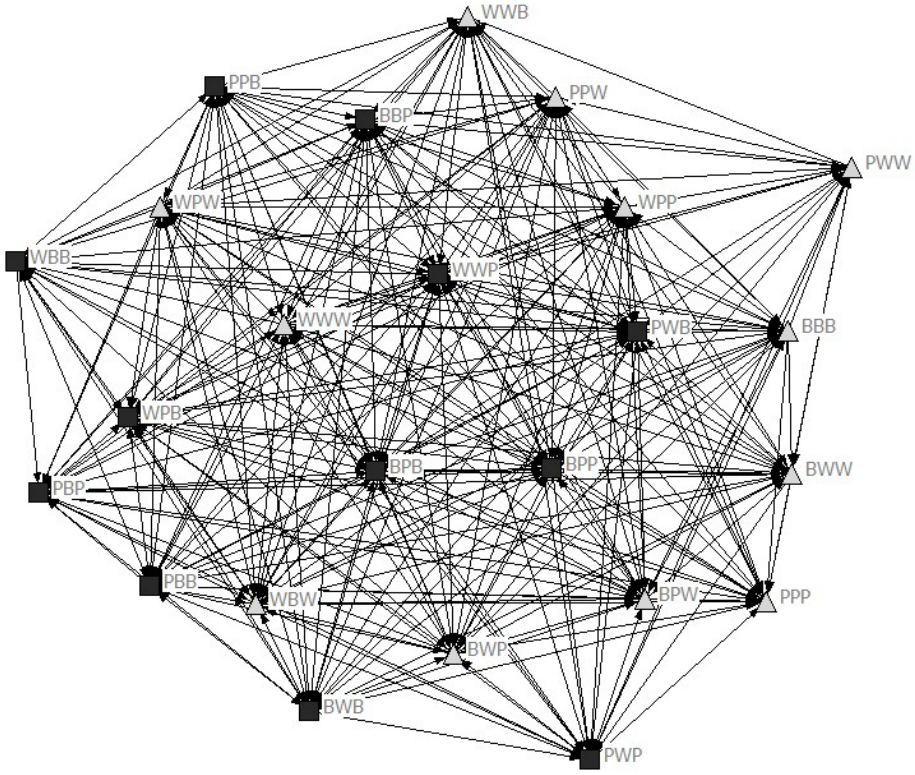

Fig. 3. Video 3 network visualization. Males are represented by dark square, females by light triangles.

Discussion

This series of "collisions" among the individuals of *Velia gridellii*, observed under natural and laboratory conditions, is for the first time named "contact behaviour". Other kinds of contacts among specimens in Gerromorpha, such as the frequent bodily encounters with adjacent members of the group "Trafalgar effect") in the the sea skater *Halobates robustus* (Gerridae) as response to the approach of a predator (Treherne and Foster, 1980, 1981), seem to represent a clearly different behaviour.

The analysis of the networks representing the contacts between specimens of this aquatic insect, did not allowed to evidence any difference between males and females, neither in their degree of connection with other specimens, nor in the role they played. The meaning of this behavior, which is normally observed in this species and has been observed in several other species, such as *V. currens* Fabricius, 1794, remains to be explained.

However, the univoltinism of *V. gridellii* (Cianferoni & Santini, 2012) with mating in the early spring (pers. obs.) seems to exclude that reproduction is involved with this behaviour, observed for the entire period of activity of this species.

Acknowledgements

I thank Andrea Fortunati (Florence, Italy) for the HD videos; Sara Storri (University of Florence) for help in preparing the spreadsheets; Giacomo Santini and Alessandro Cini (Dpt. of Evolutionary Biology, University of Florence) for the help in the analysis.

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5. CONCLUSION

Velia currens (Fabricius, 1794) and *V. gridellii* Tamanini, 1947 are two Alpine-Apenninic endemic semi-aquatic bugs (Gerromorpha), belonging to the family Veliidae (Chapters 2 and 2.1).

Most of the available ecological and ethological studies on the genus *Velia* and the relative family, referred to species in Northern and Central Europe (e.g. Mielewczyk, 1980; Murray and Giller, 1991), whilst little or nothing was known about the more southern taxa (Cianferoni and Santini, 2012) (Chapter 2.2).

Therefore the aim of this research was to begin to fill this gap through the study of the ecology and behaviour of these two species. This choice was mainly made due to the importance of these two taxa (endemics), for their taxonomical stability (valid species), and obviously for the lack of previous research on their ecology and behaviour (Chapter 3).

The two case study species are in fact valid and taxonomically well defined species by several features (mainly male genitalia). Simplified external characters and an identification key were firstly defined to allow for an immediate field classification of the two species; essential for ecological and ethological studies (Chapter 4.1).

From the analysis of the morphological characters of all the taxa belonging to the subgenus *Plesiovelia* Tamanini, 1955, it was possible to identify two distinct groups of species: a W-Paleartic centered one and an E-Europeo-Asiatic centered one. *Velia currens* (Fabricius, 1794) belongs to the former and *V. gridellii* to the latter. We can almost identify a first sympatric area among the species belonging to the two groups matching well with the range of the two case-studies (Chapter 4.2).

No evidence for multivoltinism was detected in either species through an investigation of their life-history. Univoltinism may be the norm for these species of *Velia* in northern Italy, although the possibility that different generations may coexist in more southern populations was not excluded. However, laying and/or hatching of their eggs occurred over a long period of time as early-instar nymphs and adults co-occurred over much of this period of study (Chapter 4.3).

Nymphal development was presumably affected by temperature (faster developmental rates were observed at low/medium altitudes, where the water and air were generally warmer), consistent with previous observations on the Central European species *V. caprai* (Murray and Giller, 1991; Ditrich and Papáček, 2009b) (Chapter 4.3).

Although their distributional ranges completely overlap on a large spatial scale, the two species co-occurred only rarely at the same sites and the degree of co-occurrence was lower than expected by chance. The actual mechanism behind this pattern remains uncertain and may range from competitive exclusion, to habitat-driven segregation based on an unknown environmental factor (Chapter 4.3).

Winged specimens were rarely recorded in both species even lower than that reported for other *Velia* species (e.g. Brinkhurst, 1959). A significant dependency on altitude was found for *V. gridellii* but not *V. currens*. An important point worth noting was the presence, during summer, of adults of both sexes hidden under the stones of dried-up streams. These specimens seemed to be aestivating in a state of lethargy (they remained completely immobile and did not initially responded to external stimuli when uncovered). It is hypothesized that the ability to aestivate, coupled with the ability to walk from one site to another (cf. Ditrich and Papáček 2009; Cianferoni and Santini, 2012) may reduce the advantages associated with producing winged forms and account for the low rate of occurrence of macropterism in these species (Chapter 4.3).

The descriptions and SEM images provided in an ensuing study constitute the first data on hairy structures in *Velia currens* and *V. gridellii*. This analysis was a necessary pre-requisite to the study of grooming behaviour (see Chapter 4.5).

The comparison between the two species and (when possible) with *V. caprai*, the only other known species of the genus, revealed only minor differences, confirming a substantial homogeneity within the subgenus *Plesiovelia* Tamanini, 1955. The discovery of a double layer of microtrichia in both analysed species led us to detect them in *V. caprai* too, even though only a single layer had previously been noted (cf. Andersen, 1977). We reported for the first time in the genus *Velia*, and in the Old World Veliinae, the presence in *V. gridellii* females of a structure corresponding to the grasping combs already described in males. A similar structure was not identified in *V. currens*. This difference may also be relevant for a better understanding of the relationships among species belonging to this genus. The presence of this structure only in *V. gridellii* supports the idea that these two species, although both being Alpine-Apenninic endemics, may probably belong to different groups of species (cf. Cianferoni and Mazza, 2012). Finally the lack of this comb (possibly because of secondary reduction) in *V. currens* and *V. caprai* (cf. Andersen 1982) also seems to suggest a greater affinity between these two species than with *V. gridellii* (Chapter 4.4).

The “grooming behaviour” consists of a series of regular tidying and cleaning actions, performed to tidy the water-proofing hair layers throughout the body surfaces (cf. Andersen 1982) and to maintain them free from debris. Results of a preliminary study showed that this behavior may be highly variable even within the same species, with some steps sometimes being skipped. Interestingly, occasional observations carried out on mutilated specimens showed the occurrence of cleaning movement also on missing legs, suggesting that once the “pattern” has started, this action is not modulated by way of feedback from the area that has been cleaned.

The behaviour is extremely similar in the two species, the only noted difference is the different number of passages over the antennae (less in *Velia*

currens and more in *V. gridellii*) during grooming. Considering that these two species are phylogenetically distant (cf. Cianferoni and Mazza, 2012), this behaviour is probably a plesiomorphic character, such as has been noted in the subgenus *Plesiovelia* Tamanini, 1955.

Finally the observation of the approaching of the rostrum to the rubbing tarsi of both species is consistent with Andersen's observation (1976) of *V. caprai*, suggesting that it is related to the removal of debris and water drops from the "grooming structures" by the rostrum. However, a different hypothesis, i.e. that the rostrum may produce some hydrophobic secretion (cf. Brinkhurst, 1960; Perez-Goodwyn, 2009) that then can be spread on all hair layers by the grooming structures, cannot be ruled out (Chapter 4.5).

A peculiar behaviour, observed under natural and laboratory conditions in *Velia* spp., consists in interactions ("collisions") among the specimens and is named "contact behaviour". Preliminary observations on *Velia gridellii* Tamanini, 1947, through the analysis of the networks representing the contacts between specimens of this aquatic insect, did not allowed to evidence any difference between males and females, neither in their degree of connection with other specimens, nor in the role they played.

In conclusion, the results presented by this research help to shed some light on the ecology and behavioural traits of these two *Velia* species, of which very little was previously known. Finally, besides furthering our knowledge of these species, a better understanding of their biology may help us conserve these organisms, given that the combined effects of restricted distribution (endemic to Italy *s. l.*) and the increasing effect of humans upon freshwater habitats pose a serious threat to their survival.

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